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OUTLINES OF
SCIENTIFIC ANATOMY

OUTLINES OF SCIENTIFIC ANATOMY

For Students of Biology and Medicine

Designed to Supplement the usual Textbook Teaching

BY

Dr. WILHELM LUBOSCH

Professor of Anatomy in Würzburg

With 66 Illustrations

Translated from the German by H. H. WOOLLARD, M.D.

Professor of Anatomy, University of Adelaide;
Late Assistant Professor of Anatomy, University College, London

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Preface to the English Translation.

It is my desire that the English translation of my book should be prefaced by the following brief statement.

In the first place I wish particularly to point out that this work is intended, as is indicated in the title, for students rather than for teachers of anatomy. If teachers, none the less, find within it something new, or at any rate presented in a new form, it will naturally give me great satisfaction. I desire also to emphasize the fact that the contents of my book are at variance with the usual presentation of the subject in the lecture room, only in so far as the frontiers of the science of anatomy, as described by me, are extended beyond those permitted to the lecturer by the vastness of his material. It should also be obvious that the contents of this imaginary lecture are in no wise intended to form the introduction to the actual teaching of anatomy. How and to what extent the teacher makes use of what is here presented, is for him to determine ; I have not regarded it as part of my task to define the nature of anatomical instruction embracing the whole of scientific anatomy and presenting at the same time the whole of the material. On the contrary, I desire emphatically to remind my readers of the omission, to which allusion has been made in the preface to the German edition, of all account of the organs. Until the second part, upon which I am now engaged, appears, the present portion is to be regarded as a torso. I trust, therefore, I shall not be criticized for a lack for which I have expressly begged the indulgence of my readers.

For the reception accorded to my book, both in Germany and elsewhere, I am most grateful to my kind critics. Nearly all have been kind enough to recognize the justification for such a book, and the good which may result from it. The judgment of other anatomists is of the first importance, for they are confronted daily by similar problems. For this reason they are to be regarded as experts. Mine has been the great pleasure of finding that the majority of these expert critics have not withheld their praise, and I have gratefully noted for further consideration such criticisms as they have uttered.

Of the magnitude of the faults of my book in matters of detail, I am fully conscious ; but these faults are not of the matter of the book, but lie in the form in which the matter is presented, which by its very nature must of necessity make a heavy call upon the reader's attention. It is inevitable that certain things contain problems of great difficulty, and as a result any such book as this must be studied with serious reflection and cannot be regarded as light reading. To meet the wishes of my English translator, I have deleted certain passages at the commencement of the work, which appeared to him to be of too abstract a nature, and must refer my readers to the unabridged German text in paragraphs 3 to 6 of the German edition. With these exceptions the translation differs in but few points from the German original. Some few passages I have revised (particularly paragraphs 29, 61, 63). A few errors have been corrected, and references to recent literature have occasionally been inserted in order to bring the bibliographies up to date. My sincere effort at a presentation of the science of anatomy within its widest limits from the purely morphological standpoint, my attempt to differentiate in theory between the morphological and the physiological view, however closely associated they may be in practice, has been followed quite recently, to my great pleasure, by a number of similar attempts in the domain of pathology.

We all know that the development of science is not ruled by the pen, and that every well founded result of research is woven into the sum of scientific knowledge, by whatever methods it may be gained. Science is no combat, but a noble competition of which the prize is truth. It is recognized to-day, as it was once long ago, that in the study of form, too, there is a great basis of truth. But we must not forget that here, too, theory is as nothing without practice. To the worker in morphology a boundless field is still open. It is my hope that this work of mine, in the course of the longer journey upon which it is now entering, may reach one or two who may be spurred by it to practical work in morphology.

Dr. WOOLLARD has undertaken the difficult task of translating my book into English. It is not an easy thing to render faithfully a scientific book conceived in a foreign language, but he appears to have succeeded in doing this. Therefore, I would like to express to him also my sincere thanks.

W. LUBOSCH.

Würzburg,
March 12, 1927.

Preface.

It is the function of the German universities to teach not only the bare essentials of knowledge, but also to show the real scientific bearings of one group of facts on another. This applies to all faculties. Medicine is no exception. The individual case serves the clinical teacher as the starting point for a discussion of therapeutics, and it is not possible to lecture on physiology, pathology or pharmacology, without raising various fundamental theoretical aspects. Human anatomy seems to be the only exception to this, for here the immense mass of facts dominates the instruction. The scientific questions which it raises remain untouched; the scientific enthusiasm of our best students remains right through anatomy unawakened, or if it is present it is not satisfied. And anatomy is so richly endowed to awaken the enthusiasm of the student.

Whoever teaches in close contact with the students and meets them in the laboratory, knows that the students have a longing for a more stimulating presentation of anatomy. The student has, if I might cite my twenty years' experience of teaching all aspects of anatomy, always exhibited this. In the year 1921 I published a small pamphlet (on "The Problem of the Method and Reform of Anatomical Instruction," Jena, Fischer) in which I put forward the view that we would do well to give the lectures in our science another form, and to teach the ordinary facts by dissecting, by short courses, by conversation and demonstration. The content of such lectures I had only indicated therein in a general way. The working out of the details which I have had in mind for many years past has been left undone. Hence this book.

The book is only a sketch, since even in this more abstract territory anatomy is never abstract but must be learnt from concrete objects. Demonstrations would be required for a course of lectures such as are indicated in this book. Perhaps no other course would need such a range of objects for demonstration as this. This I know well, and have only to lament that to me the possibility of converting them from a paper record to living fact has not been offered by our faculty. So I must leave it in the printed word and wait and see if, how, and where it wins life.

The presentation must remain an outline for the further reason that a more detailed examination of the questions raised would need a book many times the size of this. Here the question naturally arises whether a brief presentation can be scientifically justified at all. One can naturally do this only when one is sincere with oneself, and sees quite clearly where scientific fundamentals arise in question, and where in expectation of new facts we must be careful with our judgments. When this is prominent throughout and the literature is introduced, then a brief treatment of the subject appears to me possible and justified.

The book, however, is not only a sketch, but in an important point imperfect. The reader would notice this deficiency even if not expressly remarked. The presentation of the anatomy and the embryology of the systems and organs demands a large space, within the framework of every course of lectures. This presentation should follow after paras. 71 and 83. It is, however, clear that a deductive presentation of the form-principles of anatomy and embryology either demands a book for itself, or, if it had been joined to the present work, must have postponed its appearance for a long time. This addition is already planned, and I am committed to its publication. This separation of the material could, however, be undertaken without injury to the unity of that which is now printed. It is possible that the presentation of the subject has even gained an added emphasis thereby.

From what has been said, it follows that this book cannot and does not purpose to teach human anatomy as such. Its use presupposes some knowledge and study of the facts of anatomy, such as would be obtained from a good textbook, and particularly from practical work. This limitation of the book is expressed in its title. For these reasons I have been sparing in the use of illustrations. In so far as they have not been borrowed from other works with or without alterations, I have prepared the whole of them myself, and in the style which I have adopted for my lecture illustrations. They are schematic and much has been inserted in them. They are diagrammatic pictures developed from natural preparations. It was necessary to make my originals technically fit for publication. Herr FABER, the scientific draughtsman of the firm of Sturz [up to para. 71], and Herr W. FREYTAG, the university artist [to para. 83], have done this admirably. Figures 57 to 64 are my own work.

The literature has been extensively surveyed, and has been arranged with a double object in view. For the further investigation of any particular point, the necessary literature is cited in the bibliography of each section. The most important literature on any particular subject is indicated by a star opposite the author's name.

The literature used extends to 1924. As far as possible I have made it as complete as seemed desirable to me. It would not have been worth while to aim at actual completeness. Dr. Brandt, of Freiburg, deserves my thanks for help in reading the proofs. Particularly I wish to thank the publishers who, though they had a legal claim for earlier publication, in no way hindered the preparation of this book, and in all respects freely met my wishes.

May my work awaken in the reader the same joy in human anatomy which the constant concern with its problems has brought me.

W. Lubosch.

Würzburg,
July 14, 1925.

Translator's Note.

The author has expressed in his Preface to this translation of his book that with few alterations it follows faithfully the German text. It has been the aim of the translator to perform this task as well and as honestly as he was able. His difficulties, and they were many, were always resolved for him by the masterly knowledge of Mr. J. A. Wilks, of University College, London.

The inducement to perform this difficult and laborious work of translation came from the realization that Professor Lubosch had conferred on Anatomy a scientific dignity and importance that are perhaps not realized in many Medical Schools in England. If the translator should have helped towards a fresh realization of the importance of Anatomy, then his labour will not have been in vain.

H. H. Woollard.

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OUTLINES OF SCIENTIFIC ANATOMY.

Introduction.

The Extent and Nature of the Conception, Science—Position of Anatomy in the Scientific System.

(1) The Extent and Nature of the Conception, Science.

Para. 1. Popularly science is understood to indicate all the knowledge which we have at one moment on a definite subject. This is correct only in so far as a knowledge of facts belongs to science, and of course in a negative as well as a positive sense. In the negative sense, because when we observe phenomena as isolated events and cannot connect any particular occurrence with another, this defect, in so far as it can be determined to be such, may be regarded as knowledge.

Science in a logical sense is, however, more than the sum of knowledge. First, when we proceed by our mental processes to the linking of fact and process we attain something which we may call scientific. By our mental activities we are led to judgments, valid and logical, of facts and processes. These judgments are knowledge. Knowledge alone forms the content of science (Jahn).

Each science includes, firstly, a definite area of knowledge ; science must therefore first of all be complete, i.e., it must include all the knowledge of its particular sphere. The knowledge must be lucid and transmissible in unambiguous terms. The principles by which we judge phenomena and processes must be uniform and immutable.

One and the same object, as for example the brain, may be the subject of investigation by numerous sciences (anatomy, physiology, psychology). But if one insist on the limit of a particular science then anatomy cannot include the objects of physiology or psychology.

Finally, the knowledge must be arranged in a systematic manner. This will differ for the various sciences, and indeed in each science may proceed from different standpoints.

However, whatever method be chosen this must be adhered to throughout, if a logical science is to issue. We might, therefore, define a science as a "perfect whole of similar lucid knowledge arranged according to a uniform plan."

From what has been said, important consequences arise which affect the relations of science to the objects it investigates, and also for the further progress of science. In regard to the first point, it is to be observed that the ultimate object of science is to submit all phenomena to the operations of the mind; ideas, judgments and conclusions, system and order, lie not in the phenomena themselves, but are imposed on them by our thinking. It is questionable if the conception of order has any validity apart from our thinking. The essence of science is the subjective element, which, because it has been attained logically, has therefore general validity. Our knowledge is thereby brought into intimate relation with the phenomena of experience, and the agreement between knowledge and experience is what we mean by scientific truth (Jahn).

Since new experience and thinking may carry us to new knowledge, scientific truth cannot be regarded as absolute, but it is only by the scientific method that truth can be verified. Truth is by no means furnished only by science, since the human mind has besides its logic, its æsthetic and ethical power. Truth may be apprehended through these too. Art shows truth through the beauty of form [para. 38], religion apprehends truth by means of the parable. But only science can verify truth.

The definition of science implies the necessity of further progress. Perfection can never be reached. Science ever grows by new discoveries, and the treasury of knowledge is increased. The lucidity of our knowledge is thereby rendered dependent upon circumstances, and though it may be obscured by new knowledge, yet it is again made clear by the progress of science. The struggle to attain completeness acts as a stimulus to progress, and even leads to the formation of a new science. Anatomy only becomes a science after it has freed itself from the physiological considerations of the organism, and insists on analysing the form of the organism from a purely morphological standpoint.

Finally, the possibility of an improved order of knowledge opens a way to the perfection of science, e.g., numerous organs of the body, whose classification was before doubtful, can now be brought together as organs of internal secretion on functional or genetic grounds.

The progress of science is inherent in its definition. Evolutions such as have occurred in human history have no counterpart in science. Science is characterized by a steady progress, which not only adds but also rejects and begins again. It frequently returns to past observations which have been forgotten when its progress has made possible their evaluation and place in relation to knowledge.

The progress of science often appears to be the result of the division of labour. This, however, is rather the result than the cause of scientific progress. Its progress rests mostly on the investigations and the thinking of great individual scientists, and it is the effect of such men to open up new paths which start investigators off in new directions. And herein arises specialization. It is only the limitations of the human mind that prevent domination of the whole field of science. What is possible to the human mind is best seen if we contemplate the great masters and ignore the many tedious little ones.

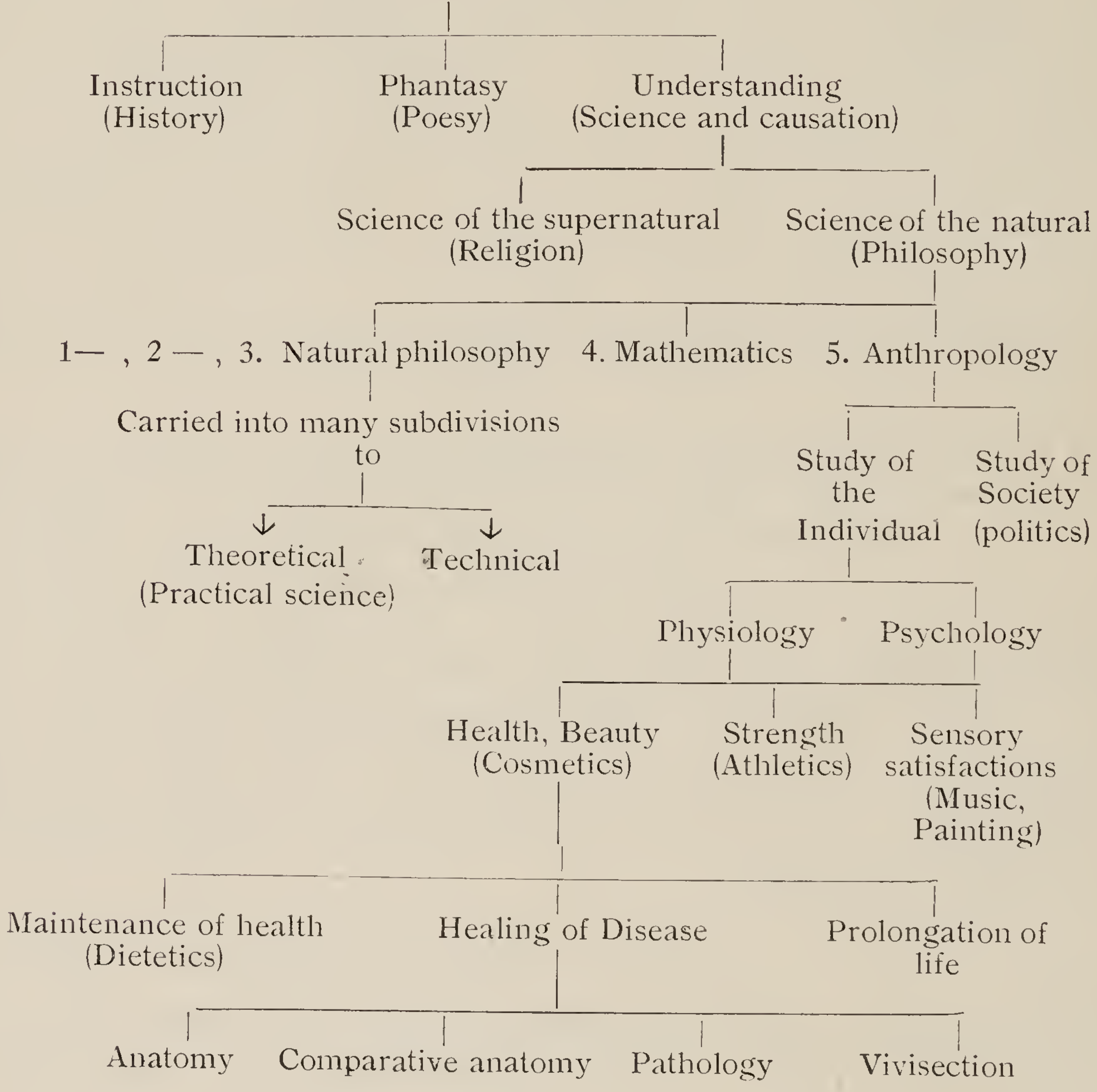
The progress of science is often affected through fashion. Fashion is based on the herd instinct of man and mistakes the appearance for the thing itself. Imitation of French fashions played a large part in the art and science of the eighteenth century. Recently it has become the fashion to imitate American ideas, such as concentration on the immediately useful and their ideas of organized work. The history of science also shows that the opposition to fashionable ideas is often justified after a very brief interval. It is often not easy to distinguish truth from fashion. Young men of science need not be ashamed of the reproach of being old-fashioned provided they follow honestly their inner bent.

Para. 2. The classification of science is sometimes regarded as an important matter. It is, however, only of subordinate value even if it were wholly possible. Artificial classifications are based on one or two external features, or simply adopt a grouping. For this very reason they often accomplish much. As an example we may give the classification of Francis Bacon, since it was one of the earliest and one of the most complete.

A natural and adequate classification would be based on some inherent feature of the objects of the sciences themselves. From what has already been said it will be apparent that this is possible only in a very limited degree. One such classification is to divide science into real knowledge (a posteriori), and ideal knowledge (a priori), since this method harmonizes well their content and method (Becher, Schopenhauer).

Sciences of the "a priori" type are philosophy and mathematics. Their objects are ideas, their content lies alone in ideas, and their method is that of deduction. Sciences of the "a posteriori" type find their objects as real events in the outside world; their content is experience and their method induction. In the last resort, however, each experience is possible only through "a priori" ideas, and so such a classification does not get to the root of the matter.

The Inquiry of Learning.


Instruction (History)
Phantasy (Poesy)
Understanding (Science and causation)
Science of the supernatural (Religion)
Science of the natural (Philosophy)
1— , 2 — , 3. Natural philosophy
4. Mathematics
5. Anthropology
Carried into many subdivisions to
Theoretical (Practical science)
Technical
Study of the Individual
Study of Society (politics)
Physiology
Psychology
Health, Beauty (Cosmetics)
Strength (Athletics)
Sensory satisfactions (Music, Painting)
Maintenance of health (Dietetics)
Healing of Disease
Prolongation of life
Anatomy
Comparative anatomy
Pathology
Vivisection

The "a posteriori" sciences, which are, of course, the great majority, have suffered from many diverse systems of classification, e.g., concrete and abstract, nomothetic (that is those which carry us to a knowledge of laws), idiographic (those which are satisfied with mere description), natural and cultural science, applied and pure science. All these have some descriptive application, but are without any real value. History shows that there is nothing purely descriptive. Comparative anatomy knows no laws (at most it recognizes rules); the study of descent need not include practical application though it may do so by expressing the position of man and the value of race. Anatomy can deliver valuable judgments on importance and non-importance, on the needs of life, the value of organs, apparatus [para. 15]. The most valuable classification is that into biological and natural sciences coinciding with the distinction between the physical (the body world) and the psychical (the mental qualities).

Even this does not carry us very far, for, on the monistic principle, anatomy, physiology, zoology and psychology must go together. Numerous mental sciences, speech, philology, history, æsthetics, need the natural sciences, and especially do they require anthropology.

It is more important to realize that all the sciences are closely related than to worry about attempts at artificial classifications. This must be so, as has already been pointed out, all sciences are based on the logical nature of their ideas, and these ideas partly overlap in content. Therefore every science has more or less contact with every other science; it may be in regard to object or in regard to method, and moreover in regard to the effect that its advances may exert on other sciences. Philosophy can be regarded as including all the sciences within its scope. Mathematics invades or rests upon all the other sciences. In the accompanying figure (1) these relations are expressed in the form of a diagram which illustrates particularly the relation of anatomy and physiology to other sciences.

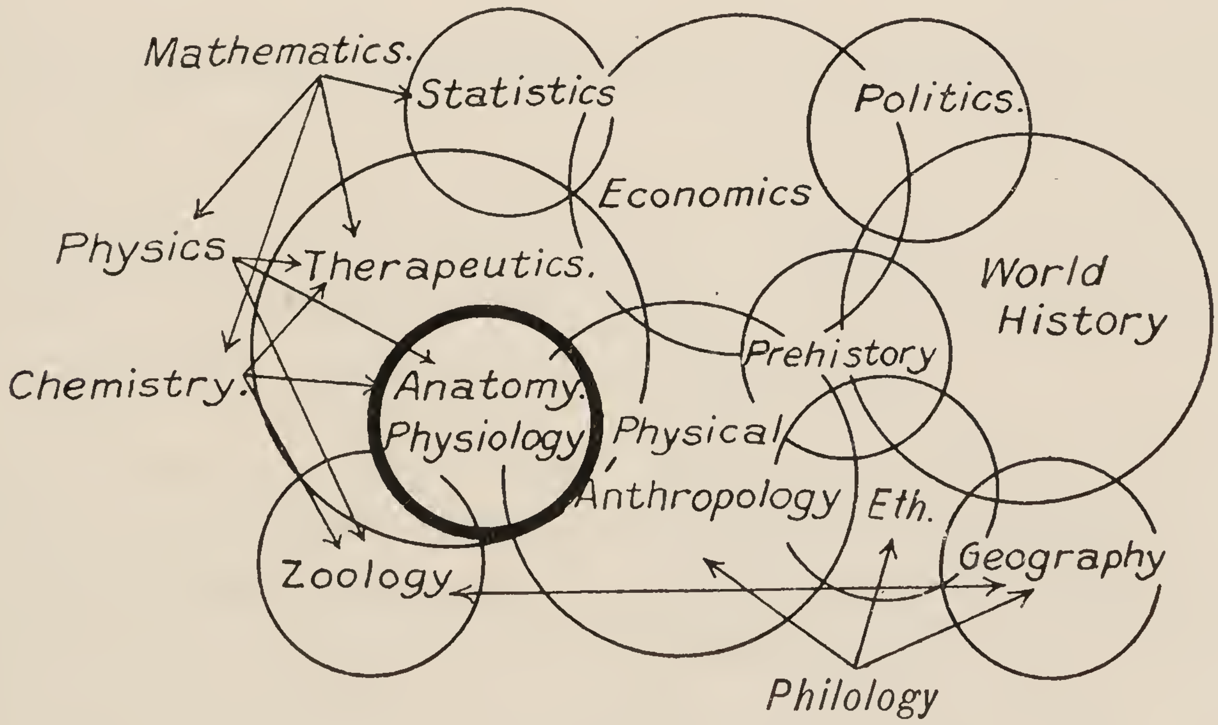


FIG. 1.

Out of this unavoidable relation of all sciences arises the necessity of considering precisely the field in which a science strives for complete mastery. All the individual sciences are gathered together in a German University, though the term university once implied the idea of general study. It was "Universitas Magistrorum et Scholarium." In the expression "Universitas Litterarum" the idea of the unity of all knowledge is now enshrined.

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(2) The Position of Anatomy among the Sciences.

(A) Anatomy and Philosophy.

Para. 3. Philosophy, which includes all science, investigates above all "What can I know?" (theory of knowledge) and "How can I obtain knowledge?" (logic). It also investigates metaphysical questions such as "What shall I do?" "What can I hope?" "What is man?" It is therefore something more than merely the results of science. Anatomy, like other sciences, must be affected by philosophy, and be assigned to a place in the philosophical system. Before we can assess the effect of philosophy in regard to these questions we must first, in view of the limits of our knowledge, inquire how that knowledge is obtained and related. In this way alone can we answer a great number of most important questions. (In the sphere of theory of knowledge: life, organization, individuality, form, change, causality, formation of systems; in the sphere of logic: methods, e.g., the comparative, the experimental, the descriptive). In regard to metaphysics it is certain that ideas of descent and heredity, anatomy, anthropology, and studies of race have been made often the basis of conceptions of man's place in nature, and consequently of conceptions that enter deeply into questions of metaphysics.

To Kant's philosophy we owe two very important results for natural science:—

(1) The empirical reality determines the scope of our investigations. It offers infinite scope within the limits of the perceptible and, by means of our imagination, even beyond. Within this limit, perfect certainty of the investigators reigns, a strict mechanism governs and causality applies inviolably. There are only physical processes; all is explicable that is perceptible. The limits of the intellect are those of the world (Schopenhauer). There are implied, however, along with this:—

(2) Limits to experiential science. All that exists only in thought falls outside this province. An entity, as a content of experience, is only an aggregate of parts standing in most complicated relationship with one another. As a content of thought, the entity is a thing superior to the parts fusing them together. In experience there can never be an effect without a cause. In thought a first cause can arise.

Definite conclusions necessary from the standpoint of thinking are the following: existence of a soul as substance; unity of my ego as individuality; first beginning of the world; last unity of the organism; chiefly, however, necessary as judgments on things in order to be able to join them into a single representation (for example, the judgment that the regulation of the organism is purposeful). They are as false when applied to the facts of experience, since they can only be thoughts, as they are compelling regarding our minds. Here arise insoluble contradictions (antimonies); the same statement is true (for thought), but at the same time is false for experience. These antimonies play a rôle in some of the above-mentioned questions [para. 14].

Schopenhauer's philosophy contributes to science and anatomy three important ideas: (1) That of the will operating in all being, not so much as an all-pervading quality of matter, but as an all-pervading desire, i.e., an activity that approaches the universal soul in the teaching of Spinoza and Goethe. (2) The new significance he can give to the Platonic ideas. They are no longer the eternal antecedents of appearance, but in an additional sense to that which they have in Plato, they have visibility, apprehensibility, and of course such as are only accessible to æsthetic (artistic) perception. They are, of course, embedded in the object-world, but it goes without saying that they are not necessarily contained in every perception. It is on this that Schopenhauer based his distinction between actuality (everything objective and therefore the ideas) and reality (what actually exists but at the same time can be contemplated objectively), a distinction which is often explained otherwise (cf. Becher). (3) Finally, Schopenhauer carries into science the fundamental distinction between ætiology and morphology ; two ways of considering an object due to the fact that our understanding applies the law of reason in different ways, according to whether it is a question of judgment on the necessity of a particular form, or the necessity of a variation (more exactly), (para. 24). This twofold arrangement is preferable to the division of the sciences of the living under the term biology, and is implicit in the speculations of Schopenhauer. As in his philosophy life is only different in degree, not in kind, from other objectivations of the living ; the limitation of biology is therefore something much less characteristic than that separation which runs through the whole of nature. For morphology corresponds to the formal, to the structural, the architectonic (termed the architectonic principle by Raubner and Rauther), while ætiology corresponds to the dynamic (Rauther's technical principle). We accept this distinction, and hold it fast, since we regard anatomy as the science of form. Anatomy has already been described as morphology by Goethe, and later by Haeckel and Gegenbauer.

Para. 4. Not only the origin and limits of our knowledge need scientific proof. We must also investigate the processes by which we arrive at the order of knowledge, from the elements of experience and thought. This is the task of logic.

The starting point of experience lies in the single perceptual representation (herein we will neglect the psychological differences between perception, conception, idea, which are in part very obscure and in part very artificial). (cf. para. 6 ff., Jahn.)

Whenever we receive a number of individual impressions of like nature, we recognize through the elementary mental processes the like and the unlike and arrive at a general idea (e.g., negro). In this all the elements common to the conception, and therein like to one another, are fused into a single picture (body colour, curly hair, thick lips). Such general ideas are "heart," "liver," "vertebral column," "ribs," "brain," "skull." These general ideas are distinguished from the individual impressions, in that they no longer contain the specific characteristics (such as the seven cervical vertebræ, or this particular heart belonging to a particular body). They have, therefore, the features which we ascribe to conceptions.

Conceptions are nearly related to general ideas, but they are distinguished from them, however, in that through an act of judgment the scope of one general idea can be distinguished from other general ideas of like degree and from general ideas of still greater degree. So the content and scope of a conception such as "negro" is distinguished from the larger conception of man (extent) and from the like conception of white race or mongol (content). The formation of concepts, therefore, goes hand-in-hand with abstraction. By further omission of that which is not common to all, from the conception man (similarities in all men), primate, mammal, vertebrate, gastreada, metazoon, the essence of life can be abstracted. By this abstraction the extent grows but the content diminishes. None the less the starting point of every conception, even the most all-embracing, has always been at some time observation. A conception, which has been arrived at without observation, belongs accordingly not to the experience of science (for example, entelechy).

The scientific formation of a conception is often impossible where the observation gives no clear definition (for example, "gland"). Conceptions and definitions can never arise from individual impressions which admit of no subdivision ("individual," which is always one). Conceptions are the real nucleus of science. They are the true currency of thought. Without the conception, "liver," the scientific description and comparison of the organ would become impossible, since every generalization would be lost in an infinity of detail, evaluation would be impossible owing to the cumbrous nature of the material work. Conception is a bridge of thought by means of which the contemplation of a thousand things is facilitated and even made possible (Jahn).

The judgment, co-operating in the formation of concepts, illustrates a higher level of thought. This is clear in the concept itself, which can always be repeated in the form of a judgment. "The negro is a black man." "The heart is the central organ of the vascular system." Such conceptions which only show the way, in which the extent and the content of conceptions have been won, add nothing further to knowledge. This first appears when in a judgment two conceptions are joined together (for example, negroes and head-form—the negro is long-headed; the right auricle and the heart sinus—the right auricle corresponds in part to the independent sinus venosus of the Selachian). These judgments fuse; they are synthetic. They lead to high levels of scientific knowledge, are therefore characteristic of the progress of science, and are the form in which new knowledge must be communicated. The description of the human body is a continuous series of such judgments.

We take a further step in knowledge when we fuse together two judgments. This conjunction is described as causation. The first judgment (cause, ratio) is the basis of the validity of the second (consequence, sequence).

For example, when a gymnast pulls himself up he contracts his biceps, or when the musculo-cutaneous nerve is stimulated the biceps is also contracted. The two types of effect are distinguished from one another. In the first the relation between cause and effect is only established on the basis of logic. It may be asked why and how such a contraction arises. The only answer is to be found in our knowledge; for the muscle always contracts in this movement, but, of course, also in many others, while in the second case the question is only from what cause. In this second case the reason is a real one (causa efficiens), for the muscle never contracts without the nerve impulse.

We are carried still further by the conclusion, when out of two premises a third follows by necessity. In the two premises one conception always appears twice, but is eliminated in the conclusion. Of the two premises one is of narrow and one is of wider import, in the conclusion the more limited conception appears as subject, the wider as predicate, so that in the conclusion appear new relationships often quite unexpected and indicating far-reaching application. This happens daily in science, and have been the means of the greatest discoveries.

For example: (1) Wherever the notochord is found it forms the beginning of the vertebral column; (2) the notochord is found in a part of the base of the skull; (3) consequently a part of the base of the skull is formed from the notochord. (The vertebrate theory of the skull of Huxley.)

Hypotheses are formed from these inferences and conclusions, and this leads us to the important processes of induction and deduction. Induction begins with observation and proceeds through conceptions, judgments and conclusions to more and more abstract knowledge, finally to general rules and laws, whilst deduction starting from abstract knowledge (rules or laws) endeavours to pass judgment upon the individual instance.

The inductive mood is of more advantage in natural science, while the deductive is of more use in philosophy, mathematics, and of much of so-called mental science. Deduction may also play a rôle in natural science as in comparative anatomy, where, from general principles, an organism can be predicted—the discovery of the hidden (Goethe). (Discovery of the premaxillary bone from the general laws of homology, comparable to the prediction of an unknown planet and its subsequent discovery.) On the other hand, the deductive method can never dispense with reasoning, least of all "a posteriori" science, since all general laws are arrived at through induction.

Especially do theories and hypotheses form the crown of science. Both are reached from induction, and are characterized by the fact that they contain a supposition. Theories and hypotheses are frequently regarded only as different terms for the same thing. There is, however, between them this essential difference. In a theory a principle is invented, according to which numerous related observations can be explained. In a hypothesis a fact or a process is supposed and a hypothetical judgment is uttered (if A is, then B is). On the validity of this judgment depends the validity of others. A theory is false, therefore, when any phenomenon does not correspond with the explanation offered. The chromosome theory of heredity is unsatisfactory if it is demonstrated that the parallel conjugation of the chromosomes does not exist, or the arrangement of the chromosomes is such that they do not definitely form precise spatially arranged groups; also, one might compare the various theories as to the structure of protoplasm. A hypothesis is false if it can be shown that the hypothetical judgment is untenable. Evolution is a hypothesis, not a theory, since it starts from the speculation that one form can transform itself into another. If it could be shown that such is not the case then the hypothesis would fall to the ground. Since this cannot be demonstrated so the hypothesis of descent is of the greatest importance. The idea of "sexual selection" is on the contrary, a theory, since the processes implied can be demonstrated in nature with certainty.

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(B) Anatomy and Medicine.

Para. 5. We have brought forward earlier important relations between the general sciences and anatomy. We now bring forward the question of what most closely relates anatomy to medicine. It is generally asserted to be the basis of medicine. The surgeon, the gynæcologist, the physician, must know what the body looks like in order to practise correctly their art, and in order to be able to make a diagnosis. Obviously it would suffice for this purpose to teach anatomy as the four methods of reckoning are taught; that is, as a sum of knowledge with which the practitioner can work, as we in our daily life, work with the four methods of reckoning, without worrying ourselves with anatomy, or with algebra as sciences. It follows, therefore, that medicine does not have much need of scientific anatomy. On the ground of observations to be made in a moment one might proceed directly to the further conclusion that even a purely practical knowledge of anatomy is not essentially necessary for the successful practice of medicine. Here is a problem not generally recognized, whose discussion will make clear to us for the first time that not only elementary knowledge, but real intimacy with anatomy, as a science, is required of every doctor. Anatomy is to be looked on not only as the foundation, but as the principal science of medicine.

This does not rest merely on the importance of the practice of medicine. It is, in the first instance, an ethical importance. The medical practitioner appears to us "as the saviour of life, and there is nothing to be compared with the immediately valuable nature of the services he renders" (Richard Wagner). Moreover, the social value of the medical profession was recognized in antiquity, at which time its aim was to preserve the health of the State and to sustain citizens fit for war. Thirdly, there attaches to the medical profession an æsthetic value. It gives the feeling of joy in one's own ability and awakens (Kraus) the disinterested striving after increase of this ability. It is to be observed in this connection that medicine concerns itself not only with the healing of the sick, but also with the maintenance of health (dietetic) and the prolongation of life (macrobiosis) as first noted by Francis Bacon.

In these statements on the three aspects of medical practice nothing has been said about its methods. The present day admits the view that methods of scientific anatomy are not generally reckoned amongst them. One can quote examples from medical practice to show that practitioners with but a scanty knowledge of anatomy have made successful doctors. The present day opposition to the alleged predominance of anatomy in the course of instruction, an opposition which is found among medical men even in the universities, seems to confirm this. Even the little which anatomists find to-day necessary for instruction is regarded by numerous doctors and physiologists as too much.

It is now very instructive that the history of medicine affords an apparent basis for this view. History shows at all times that there have been great doctors who either knew no anatomy, or an anatomy that was full of errors. It shows also very simply that if a true anatomy were necessary for successful medical work no doctor could ever have practised; for to-day there are a whole series of anatomical discoveries which were unknown to anatomy, and accordingly to the doctors of thirty years ago (for example, the bundle of His, the whole parasympathetic system, the finer anatomy of the brain, and many others).

The history of medicine tells us of immortal doctors who—even at a time when anatomy already commanded respect—employed, in addition to the all-important bedside observation and experience, philosophic theories as their chief scientific equipment.

The teaching of Hippocrates rested on the natural philosophy of Aristotle, as indeed all the ancient philosophy rested on an adaptation of the old teaching of natural philosophy. Hippocrates had only an exact knowledge of the skeleton. Galen (A.D. 131-210) knew only the anatomy of the ape, and the physiological and biological theories that governed his practice were derived from Aristotle, exactly as those of the famous Arabic and Jewish schools of the Middle Ages were. The anatomy of man was unknown to them too. In Salerno the pig was the animal dissected. Paracelsus (1491-1534), though a contemporary of Vesalius, declined to concern himself with anatomy, but on the contrary based his therapy on a system of great value in natural philosophy, which taught the unity of life of the universe (Erdmann). Man as a microcosm was joined, he said, by a thousand threads with the world at large, the macrocosm. The life force and the fifth essence (the quintessence), derived from the four basal humours, played an overwhelming rôle in his diagnosis and therapy. His teaching was followed yet a hundred years later by van Helmont (1578-1644). Sylvius (1640-1672), himself a discoverer in anatomy (aqueduct of Sylvius and the fossa of Sylvius), stuck as a doctor to the chemistry of life (Jatrochemie), and this at the time of anatomists like Malpighi, Leeuwenhoek, Swammerdam and Harvey. At the time of Linnaeus and of Newton, Morgagni, Valsalva, Scarpa, Thebesius, Vater and Albinus, the great Stahl abandoned himself entirely to the teachings of the dualistic philosophy. Sydenham (1624-1689) especially declared that a special knowledge of anatomy was of great service to the doctor, but did not equip him for the interpretation of a clinical picture, or the development of therapeutic methods. Similar views are found in the nineteenth century, and Schönlein stands in marked dependence on the philosophy of Schelling. Moreover, in a notable way in the period of dominance of bacteriology, when the value of anatomy was well appreciated, decisive value was attributed in the appreciation of disease to the struggle of the organism with bacteria, an idea quite in keeping with contemporary philosophy (Darwin, the struggle for existence).

Para. 6. It is essential in all these systems of medicine that the doctor should consider his patient, in respect to his disease, not as an object of investigation, but should intuitively grasp the form of the disease, by comparison differentiate it from other diseases, and out of his experience formulate rules for prognosis and treatment. Therefore there was, at least until the beginning of the nineteenth century, no scientific knowledge of pathological processes. Disease appeared rather as an evil being (ontology) that overtook the body.

Beside this attitude there runs through the history of medicine a second attitude. It shows us doctors who devote themselves to the very thing which these others only apparently replaced by speculations of natural philosophy—a scientific knowledge of disease processes. The sick man now became the object of investigation. For this purpose anatomy was the source of a constant stream of new knowledge in ætiology, diagnosis, prognosis and treatment. It was characteristic of it that it theorized less than it investigated the dependence of disease processes on bodily processes. Since anatomy is knitted to material things it is the necessary basis of a sound pathology.

Already among the old Alexandrians (200 B.C.) this appeared. Their work actually depended on investigation of human bodies, and it is characteristic of them that they stood in scientific relation to the atomistic theory of Leukippos and Democritus. The same was true in the Middle Ages, when Borelli, the contemporary of Sylvius, founded the Jatro-physical school. Alongside Stahl, Hoffman worked as a Jatro-physicist. At the time of Sydenham, Boerhave investigated disease according to its position and cause. This method of investigation in the hands of Virchow (1821-1902) received its final determination. The disease was recognized as a disturbance which rested in turn on disease changes of elementary parts of the body (cellular pathology). In cellular pathology for fundamental purposes it is a matter of indifference whether one imagines the changes to be localized in definite parts of the body and to definite cell groups, or refers them back to some general disease process.

This survey shows us that the expression, medicine, hitherto used alone, has a double meaning. Medicine is both the art and the science of healing. The healing art can never be taught; only the practical part can be learned. To this part belongs of course anatomy; but the healing glance, the power of observation and discernment, the knowledge of his fellows, and an inborn something alone make the master of the healing art. A bit of this something every doctor must indeed possess. Yet the art of healing is not the whole of medicine; the science of healing as a natural science of disease is indispensable. The progress of scientific anatomy has always, like the progress of all other natural sciences, been the progress of the healing art.

We may now express our opinion whether scientific anatomy is essential to medicine. The born master of the art can do without it. For him a slight knowledge of the form of the body is sufficient. It must, however, be allowed that only these chosen few should be entrusted with the handling of disease—a condition alike impossible in theory and practice. If anatomy is not of much help to these born practitioners of the healing art, yet it remains for the majority of practitioners a science which they all can learn. Even if they do not understand art they must be instructed in its handicraft as far as possible, so that they may avoid great errors and failures in the care of disease. Scientific anatomy gives to all practitioners the key by which alone they learn to look upon man as part of nature.

Heredity, origin, genealogy, constitution, race, adaptation, differentiation, development, are fundamental notions for the understanding of disease. In fact these are things which Virchow taught as the principal lessons of man. To these problems all that might be described as pure anatomical facts stands in close relation as visible expression of systems, rules, laws. Those who cry "too much anatomy" might take note of this.

This inter-relationship characterizes all anatomical facts. Each singly is subordinate to the whole. The law appears in the least fact, as the light makes the smallest particle of dust visible. There is nothing to distinguish any fact as important or unimportant in itself.

We would finally remark that if the born empiricist can get along without science, at any rate the born investigator, who may open up new paths to the healing art, must be trained in the scientific departments of the universities. We do not know who of the young men may seize the torch of science and hand it on. We ought not to allow the torch to be extinguished. The limitation of the study of anatomy often demanded to-day, would, at least in what concerns the sources of knowledge in this science, be like an extinction of the flame.

Para. 7. The history of the faculties of medicine and of anatomy within the faculties shows that anatomy has always been an excellent educative medium for doctors, and that medicine has always valued it as a science among sciences.

The older schools of medicine were soon joined with schools in other sciences, such as law and theology. Medicine formed a part of "the general study." In the oldest universities that we know, such as the Museum and Serapeum of Alexandria, this was the case (300 B.C.).

In the constitution of the medical faculty in the Middle Ages from the fifteenth century, they had two professorships at least, one for medicine and one for surgery. Later there was added a third professor for therapeutics and pathology, and a fourth for physiology. Not until the eighteenth and nineteenth centuries were obstetrics and ophthalmology and other specialities created as separate departments. Anatomy in a few universities was included in surgery (for example, Leipzig); in most others it was in a striking fashion part of physiology.

The instruction in all these departments consisted in the beginning of readings of the works of the Middle Ages. The term "reader" of to-day derives its significance and meaning from that. Boerhave was the first to work in the clinic and give instruction at the bedside about the middle of the eighteenth century. Originally the instruction in anatomy also depended on the reader, who has therefore persisted right up to the present, somewhat as a fossil endures through the ages. Yet the reader was, in contradistinction to other departments, right from the time of Vesalius, given practical duties of demonstration (the display of dissections) in Vienna and Prague about 1400, Leipzig, Tübingen, 1482. The first dissection for students took place in the University of Leipzig in 1785. In the nineteenth century this became general, and readers and demonstrators in histology and embryology were added.

The present constitution of the medical faculties, with their progressive specialization of departments, is understandable by reference to the past. To-day anatomy brings its contribution to the general stock of knowledge to its hearers in two ways in accordance with its history; firstly, as lectures, and secondly, as demonstrations. The little which it can give to the general stock of knowledge, that is not already included in zoology, botany, and physiology, scarcely finds a place owing to the lack of time. Even the full survey of its facts is limited by the demands of medical vocation which would like to have the whole of the practical requirements taught in the university.

Similar unsatisfactory conditions rule at present in the whole educational system. The cause is a general one; the desire to transmit facts instead of problems, thereby showing how real knowledge is acquired (Paulsen, Humboldt). The comparison with veterinary science shows that this subdivision into special departments is not necessarily joined up with the development of medical practice. It is the importance of the individual that leads to the subdivision of specialized departments. We will not discuss here whether this subdivision of the areas of research is also necessary in teaching.

It is certain, however, that a complete practical mastery can only be obtained by the entire devotion of each individual to the actual doing of the thing, and can be obtained only by great effort. He should get during his student days what can only be acquired with difficulty in later life—knowledge and wisdom.

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(C) Anatomy and Physiology.

Para. 8. In the foregoing pages we have touched on the boundaries of anatomy from more inclusive studies, and from those of similar range. We need not therefore consider any further the relations of anatomy and physiology. Both sciences have not only a great field in common, but indeed they have the whole of life as their range. They bring to bear on the study of living things two different points of. view, and so they may be compared to the two surfaces of a sheet of glass which is illumined on both sides.

Though in general the object determines the method, yet here is an example of the independence of method from the object. Each science has to do with a particular aspect of life, and approaches it with its particular questions, which in turn determines its methods.

These two sciences of life are distinguished from each other by the questions they raise and the methods they use. Anatomy seeks after the form (morphology); it asks "How?" Physiology seeks after the processes in the form and how they are carried out (ætiology); it asks "Why?"

This division cannot be pushed very far in practice, since the changes of form (which also belong to ætiology) depend intimately on what determines form. The question of the "how" of form at once calls forth the question "Why?"

Obviously physiology and morphology are here very closely related. We therefore distinguish between two kinds of physiology, the one investigating the ætiological processes governing formation, the other studying the forms themselves. Embryology belongs to physiology in that it investigates processes which go on in the undeveloped organism, e.g., the behaviour of the parents during the act of generation, the behaviour of the fertilized egg and all the phases of the developing embryo. For these reasons embryology finds a place in textbooks of physiology (Rosemann). Since in practice embryology is generally allotted to anatomy, there is in these days at least no perfect separation of anatomy and physiology. They are, indeed, firmly bound together by their common investigations. In place of the usual subdivision into two we shall follow Rosemann, who has furnished us with a biology in which he makes three subdivisions, somewhat in the following manner:—

BIOLOGY.

(1) Morphology.	(2) General portion.	(3) Physiological portion.
[Inquiry into form, Rosemann.]	[Inquiry into development and formation. Embryology and organ formation. Relative physiology.]	[Inquiry into processes, Rosemann. Real physiology.]

General form will not be further considered here, since it is the object of the subsequent pages to unfold this. We are concerned here with the sharp separation of one and three. This sharp separation of the sciences of life, into anatomy and physiology, is ultimately the expression of a development through which the human spirit has passed, in the knowledge that it is possible to investigate the whole of life. The correctness of this is patent in the history of both sciences. This history brings out how gradually anatomy has emancipated itself from physiology. For anatomy, after wrestling with its material for a hundred years, has recognized its tasks and methods, and has thus made itself an independent science.

Para. 9. The natural sciences at the time of Bacon knew no independent science of anatomy. The position allotted to it in the scheme of the whole of science and its particular objects are set out in para. 2. Even "The Anatomy of Man," by Vesalius, which existed at this time was not capable of awakening any suspicion that in the mysteries of the human body, now for the first time disclosed, problems were set to science of quite a new type.

Vesalius' Anatomy is a textbook, and as such composed and written. According to the measurements of to-day it comprised something of about the extent of 500 printed pages of textbook size. Moreover, it possessed text illustrations, a valuable gift of German pedagogy. The work functions as a textbook in the widest sense, i.e., to demonstrate the structure of the living human body. Every help available at the time was pressed into service. (Dissection, embryological investigation, study of living man, the bodies of animals, and vivisection.) The physiological view-point would seem to be firmly held, but more as a purpose than as the consideration of the individual structures. The latter follows what we call to-day the systematic method (bones, ligaments, muscles, etc.); here, however, Vesalius differs from us moderns in that he brings together parts foreign to our systems, such as a grouping of cartilages (joints, nose and larynx, etc.). Moreover, he is in part influenced by functional considerations. He therefore brings together the musculature, the nerves and blood-vessels of the alimentary tract. Finally, he attaches great importance, as a means of demonstration, to the method of section, e.g., the layers of the muscles. A systematic principle runs through this too, e.g., the plexus is presented at the appropriate point with the nervous system, not with the extremity. The whole is the work of one who of course thought in the spirit of his time, but throughout an original genius, hindered by no ancient theories.

He belongs to his own time in so far as all anatomical forms are only to him a means of functioning. But he looks to the future in that he was the first who collected general characters of particular systems together (bone, cartilage, ligaments, muscles, vessels, skin), and the first who recognized a general anatomy, which developed later into the study of tissues, though this word was unknown to him [para. 12].

The principles of Vesalius remained at first undisputed. Albinus brought out beautiful monographs on the muscles, bones, vessels, and numerous papers on special anatomical subjects. Boerhave was the first deliberately to assign anatomy to a lower position and to subordinate it to physiology. According to him all separate significance was to be denied to it. The principle according to which anatomy should be conducted is the physiological one. The functions are to determine the principles of division in accordance with which the anatomical material is to be arranged. Boerhave proceeds as follows:—

He begins his presentation with nutrition. Next comes the nature of food. This is followed by the reception of food, mastication, the jaw muscles, teeth, and tongue. Then follows the movements of the mouth, platysma, saliva, and salivary glands, stomach, digestion in the stomach, blood-vessels of the stomach, etc.

His book, according to the notions of to-day, is only a small compendium, and finds its continuation in the great tome of Haller's Physiology. It is expressly stated in this book that the ART of dissecting (Haller knew nothing of a science of dissecting) is exclusively a means of obtaining physiological knowledge. One could know nothing in physiology except in this way. Anatomy has nothing else to do than to assist physiology in understanding the processes of the body, and in this takes its place beside mathematics and physics and other sciences useful to physiology. To him physiology is nothing else than the sum of the movements that go on in the living machine, of whose ways human anatomy can therefore afford no exhaustive knowledge. It is necessary to resort to comparative anatomy which uses the living animal, i.e., therefore the comparative physiology, e.g., that of the respiratory muscles.

The eight books of his physiology include: blood and juices; respiration, speech; brain, nerves, muscles; the senses; digestion; regeneration. The general anatomy of the vascular system, of the blood, muscles, and nerves, etc., occupies a great space. There is no complete systematic account of the skeleton, muscles, nerves, and blood-vessels. The organs are treated in extenso where they can be brought in physiologically, just as Boerhave treated them briefly. In this way many things which have only topographical relations are brought together, as for example, all muscles, nerves, and blood-vessels of the thorax, including the azygos system of veins, are dealt with in the chapter on respiration.

One realizes that many things which we include under anatomy are left out as there is no way of bringing them in. The consideration of these things would have been a departure from Haller's theme. He remarks, and no objection can be taken to the remark, "that a long description of all sorts of trivial things causes generally a nausea, especially since for the most part they have no use." One feels that this kind of anatomy must please the reader and the hearer very much. Everything that it includes clearly manifests its relations. In the territory covered there was true science, since nothing stood in isolation, and science is not a mere collection of facts but resides in the principles that bind facts together. The anatomy at that time escaped the criticism that it taught too much that was trivial. The only reproach which could be levelled at it was its ignorance of the principle which declares that what is apparently trivial may have scientific importance.

Para. 10. Two different lines of development starting in the eighteenth century increased the value of anatomy. The striving after purely anatomical knowledge which had inspired Vesalius, broke the limitations which had been imposed by a purely functional anatomy. The question of what structures in the body really looked like started investigators at this time on a more intensive study of its form with finer methods of preparation, e.g., injection, maceration, and corrosion. The general histological characters of organs became more and more known. The second influence, and this was by far the more decisive, was the conception of the form of animals as a scientific principle. The problem of form originally belonged to the domain of natural philosophy and came to anatomy from comparative anatomy.

One did not, like the physiologists and even as some comparative anatomists, as, for example, Buffon, arrange organs according to their functions and compare them as apparatus for performing functions. On the contrary, their varying form and position became the object of investigation, and this led to the distinction between functional (analogous) and anatomical (homologous) equivalence of organs [para. 29].

The use of these formal considerations did not arise suddenly in anatomy but took place gradually.

Soemmering, who followed and revivified the tradition of Vesalius, and who, as the friend of Goethe and Kamper, was devoted to comparative anatomy, by his textbook of human anatomy created a work which is in sharp contrast to the physiology of Haller. But the new aspect does not appear in his work in an unalloyed form. He describes the purpose of his book as being to show how far we have acquired a knowledge of our bodies, and he labels this a science consisting of objective, easily provable truths. He is conscious that the connection with physiology is growing looser, but is not yet able to separate entirely the two sciences. He dissents sharply from the view that the living body belongs to physiology and the dead to anatomy. He includes both within the purview of anatomy and handles his material accordingly. The boundary between anatomy and physiology no more corresponds to the boundary between the living and the dead for him than it did for Vesalius. The corpse has never created a science of anatomy. Soemmering supposed the purpose of physiology to be just the same as Haller, the understanding of mechanistic principles, that is, the investigation causally of the potentialities, structure, and achievements, in accordance with the laws controlling them. This was first clearly formulated later by Johannes Müller. Soemmering did not define the special purpose of anatomy.

His great successor J. F. Meckel did this. The four volumes by this anatomist are not only a modern work in the real sense of that term, but also one which includes the whole extent of scientific anatomy as no work before or since does. The influence of morphology can be felt right through the work. He defines anatomy as the principle of organ-forming, and for the first time differentiates it sharply from physiology. Anatomy takes its name from dissection, is derived from dissection as he says, but not because it is only dissection, as the ignorant still assert, but because it is one of the means, and the most important one, by which we obtain our knowledge of organ formation. He includes both the rules for dissecting and the scientific evaluation of the knowledge gained by dissection.

The morphology, "what we mean by the study of types and their metamorphosis," is the guiding thread of his presentation. In the first volume he gives a general account of the study of the form of the human body (corresponding somewhat to the promorphology of Haeckel [para. 48].

General anatomy, the later study of tissue, also takes a prominent position. He includes, along with the embryology, the malformations of the body and thus regards pathological anatomy as in the province of anatomy.

If we examine the important textbook of Physiology by Johannes Müller, we see what changes had come about in the outlook of physiology meanwhile. In this book physiology is defined "as the science of the properties and phenomena of the organic body and the laws which they follow." One recognizes that the employment of a substratum of anatomical knowledge still comes within their purview, but that it is relegated to a secondary place. In his book anatomy can no longer be perfectly studied. The theme is always the laws determining the processes of the body. This knowledge had been increased by experimental investigation just as the knowledge of morphology had grown by dissection and observation of living organisms. The presentation is governed by analogies and not by homologies, and this is very apparent in the description of movement.

In an anatomical textbook, walking and standing may be described in terms of the old functional anatomy, but are here related to locomotion in general (swimming and flying for example) [perfection, unity of knowledge, para. 1], and further, they fall into the larger class of laws of movement *in general* (eye muscle movements, automatic, reflex movements, associated and co-ordinated movements). One sees that anatomy has very good reasons for assigning the study of movement to physiology, for it can only give a patchy explanation of them in the way the old anatomy did, or if it strives for scientific unity it must cover the whole gamut of movement, and this would extend anatomy far beyond its territory. Physiology had ceased to be merely applied anatomy as it became more and more the mechanism of nature. With the introduction of exact methods it became a causal science, the ætiology of nature.

Para. 11. The material of anatomy increased with the growth of science. The description of an organ no longer ended with its naked-eye appearances. By decisively turning away from natural philosophy, particularly that of Schelling, who had dissipated the truths of morphology in phantasy, anatomy built up in a purely practical way a more fruitful body of knowledge of its own. In the fields of histology, cytology, and embryology, it has found its problems.

This has had important consequences for anatomy. It has remained with the fullness of experience still based on pure description. Description by itself is, however, not a complete principle for science as ætiology is in physiology. This has occasioned two great didactic difficulties; wherein lies the value of facts, if their significance is no longer found in their function? A second didactic difficulty arises from the temporal relations of these two now independent sciences. Physiology had to, and could, presuppose the knowledge of anatomy, but the reverse was, and is, impossible, unless the subject were traversed twice. The teaching of the two subjects, one after the other (even when they remained in the hands of one man, as was the case until the 'sixties) could never again be exchanged for the method of teaching them side by side and interspersed with each other, such as existed in Haller's day.

Whilst the second difficulty is, in fact, insoluble, the solution of the former is found if anatomy can be brought under a general non-functional view-point. If, in short, it returns to the conception of morphology in the old natural philosophy. This was the achievement of Darwinism. Darwin's great importance lay in the fact that he justified the morphology of the preceding years of Vicq d'Azyr, Goethe, Geoffroy St.-Hilaire, and Owen, and gave it a new scientific form, by no means unassailable. Anatomists, like Gegenbauer, applied the principles of Darwinism to the study of human anatomy, and

Haeckel, Hertwig, and Rauber did the same for embryology. These influences, however, did not affect the study of the tissues for ten years until the appearance of the work of Fr. Maurer.

Gegenbauer, like all his great predecessors, defined anatomy as the science of the form and structure of the body. By form he meant the larger classifications of systems and organs, and by structure the classification of the finer elements of which the organs were composed. The form and structure of man differs in no way from that of other organisms, though this agreement becomes more difficult to recognize the further we go from man in the animal world. It is in the determination of this agreement that the scientific purpose lies. The beauty of the science lies in the demonstration of this agreement, and in the description of the differentiation, that has led to the establishment of the human organization.

This is didactically important, since no part of the body, the grossest as well as the finest, is outside this process. What is practically important or unimportant has now the same value, and also, what may be functionally unknown or obscure may be evaluated on formal considerations. Anatomy has become the science of the morphology of man. In the understanding of the human form, morphology is what grammar and syntax are to language. Morphology is the language in which the world of form, and the human body as well, speaks to us (Rauber).

We have now followed exactly the historical path by which anatomy came to be emancipated from physiology.

However, the development of science does not stand still. Questions as to the causes of form were raised.

Right at the beginning of the investigation the question was to determine the influences which affect the form of the organism (pre-scientifically speaking)—the form-producing factors. A. Rauber was the father of these ideas. The scientific and methodical development of these ideas has been the life work of W. Roux. It is here that the conception of cause brings about a division in morphology. Alongside the physiology of function, which had till then been regarded as the only form of physiology, there now arises, as we have already mentioned, "the physiology of relations," which can only be prosecuted by the help of experiments on living animals, and which earlier was known as developmental physiology, a somewhat obscure expression, but which Roux himself has called by the name of "Entwicklungsmechanik" (experimental embryology). (Cf. the description in Roux's Terminology.)

Thus arose the need of finding a name for the investigation of the form of the whole of the anatomy of the adult body in which form will be explained by function (Braus). Though the original position of anatomy in relation to physiology has been reversed, the presentation, in principle, reverts to that of Haller. Still, this principle can only say that a certain form is capable of a certain function, while the real causes of form lie yet deeper.

The science of heredity has achieved greater significance for morphology [para. 32]. In conjunction with the knowledge that the cause of a particular form lies wrapped up in the original germ plasm, this has become the foundation of the recent science of the constitution of man. Between the science of man's constitution, which investigates the ancestral properties of the individual, and comparative anatomy, which principally looks on man as the example of a species of the animal world, stands anthropology, whose object is the investigation of the racial varieties of mankind. Just as the anatomy of the European is a particular chapter of anthropology, so is anthropology as the comparative anatomy of man only a particular problem of general comparative anatomy. Anthropology becomes an individual science by being based on comparative anatomy (Klaatsch).

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(D) Anatomy as a Special Science.

Para. 12. From the earlier statements we might still regard it as being correct to-day to define anatomy by the old name of "dissection," that is, anatomy is the science which gains knowledge by the art of dissecting. Looked at in this way the name of our science is protected from the misunderstanding frequent among anatomists themselves that they are concerned only with dissection.

This activity is by no means to be regarded as being something of little value. Though numerous methods serve and have served anatomy in order to understand the ways of the living body (special conservation, frozen sections, percussion, investigation of the living, particularly action and movements, eyes, larynx, nose, ears, with the speculum, technique of operations, serial photography, most recently cinema pictures, and, above all, X-rays), yet it must never be forgotten that the preparation of the dead animal is, and remains, the most advantageous and the most fundamental method of studying anatomy. This is shown by the fact that the doubtful results obtained by other methods can only be cleared up when this method can be employed (Hasselwander, Fr. W. Müller), and further, that inquiries in new territories, such as constitutional anatomy and racial anatomy, results perhaps uncertain and even wrong, will remain so, unless corrected by investigations on the dead subject (Lubosch).

We have said that the purpose of dissecting is to learn the morphology of man. This may be expressed in more detail as follows: Anatomy, as a science, has to do with the form of man, both externally and internally; with the form, size, position, direction of and connections with other organs; with the tissue structure and the macroscopic and microscopic features of the elementary parts.

Anatomy considers the form of the whole and its members, the form of the organs and their elements morphologically; that is, it investigates the laws which govern the arrangements of these parts in space (1). It isolates the human form as an individual instance from the totality of nature and then removes it from this isolation by rejoining it anew with the form of living things in general (2). It proceeds to judgments [para. 5] on the permanency and change of organization, to conclusions on the causation and conditions of the structure and differentiation of form (3); and to theories and hypotheses [para. 5] on the position of man in the whole of nature (4). At the same time it teaches the methods by means of which this knowledge is obtained (5).

This book is concerned with the majority of these problems, though the presentation does not altogether follow the arrangement just mentioned above. The statements marked (1) and (5) are found in the special part and the ones marked (2) and (3) are treated in the general part. The problem labelled (4) is not dealt with here because it would require a specialized knowledge of the comparative anatomy of man. For this reason the consideration of the organs and systems is omitted, as this is the subject matter of the special textbooks of anatomy. It is more important to give a brief consideration to the idea of system and the conception of "systematic anatomy," as this is of significance for a later part of the book [para. 94].

Anatomy can be treated analytically or synthetically. The analytical method resolves the body into its parts and describes them without reference to the whole. The synthetic treatment, as topographical anatomy, fuses the distinct parts into the original spatial unity. In the former method anatomy unites the parts to form higher unities, which consideration shows to be in the first place functional unities. These unities have recently been described as systems. The systems are further regarded as combinations of organs.

In this division of the body into organs and systems there are many things which are of doubtful significance and difficult to classify. The explanation of these difficulties is apparent when we consider the history of anatomy in the light of the functional considerations which have influenced it. Scientific anatomy must not pass by these difficulties, since a consideration of their origin contributes to greater clearness as to the true inwardness of our science.

The old anatomy was of course familiar with the conception of organs, but did not understand the recent ideas of tissues and systems. It distinguished structural elements (vesicles, granules, fibres) and higher forms composed of these elements. These higher unities they named systems and distinguished general systems (such extensive systems as epithelial system, vascular system, nervous system; we would now call these epithelial, vascular, and nervous tissues); and special systems (bone, cartilage, fibrous, muscular, cutaneous, serous, glandular). General or systematic anatomy concerned itself with these systems (cf. the appropriate chapter in J. F. Meckel). What the older anatomists meant by general anatomy has now become the "tissues." This explains why the study of tissues and cell is often called general anatomy, a terminology which Gegenbauer criticized, since this general anatomy contains the most specialized parts of the body. His objection does not apply to the original conception which actually included something quite general, but he is justified when he criticizes the transference of the term to the present-day tissue study. There was at that time ascribed to the systems an idea of texture which we now ascribe to tissue. In their (older) systems they had before their minds something concrete, and it is a defect of the present conception that this concrete notion has been lost with the introduction of the notion of tissues, since the idea of a concrete tissue is only obtained now from the study of organs. We miss something which used to be present when, under the conception of a fibrous system, for example, the periosteum of bone, the dura mater, the capsules of organs, tendons, fasciæ, and aponeuroses were described, or under the conception of a serous system, the synovial membrane of joints, the serous membranes of viscera, the pleura, and the peritoneum. It is very instructive to look back on the assemblage of organs, so very different from one another, in a synthesis in which all similarly constructed organs were brought together. This form of synthesis has been lost in the modern conception of tissues and is only very imperfectly replaced by the present study of general histology (tissue study).

Topographical anatomy was also something quite different from our present-day conception of the subject. At that earlier date it reconstructed the organ in its natural position out of the separate (histological) systems (cf. Meckel's book). The organs were distinguished as " simple organs " and as " apparatus " (that is associated parts compounded from simple organs and possessing more complicated functions and incapable of subdivision). Flesh is always flesh, " but a hand may be no hands." Organs were therefore the homoiomeres (homoios = like, meros = part), apparatus was synhomoiomeres. The alimentary canal as a whole was regarded as an apparatus and in like manner the sense organs. Whilst one would regard the bone or the muscle as an organ (simple) the hand would be given the rank of apparatus.

All this was naturally right so long as one did not penetrate very deeply into the structure of a bone or muscle. We know that the analysis of, say a humerus or a pisiform bone, leaves very little that we could call humerus or pisiform bone, and so also with such an organ as the brain. The constitution of an organ depends on its form and structure (a collection of different tissues). The only validity which this distinction of organs and apparatus now holds is in the value which a part may hold for the body.

It may be granted that the hand is of more functional value than the pisiform bone, but this raises very general and important questions morphologically. There is no possibility on morphological grounds of separating sharply organs from apparatus unless one uses the conception of apparatus in the sense of system as used now. As apparatus, the hand is not separate from the arm and the arm is not separate from the body. As a piece of apparatus the hand acquires no functional independence. Undoubtedly the stomach is infinitely more valuable than a phalanx, but the stomach as apparatus is no more independent of other apparatus than a phalanx is of the skeleton of the hand, and the muscles, blood-vessels and nerves of the hand.

What the anatomy of to-day describes as a system is derived in one direction from the older histological system, and in another from the " apparatus " of higher functional value of the old anatomy. The latter aspect is clear from the fact that it is still incorrect to speak of apparatus of movement, of alimentation and internal secretion, etc. When function is made the principle of classification any sharp anatomical boundary naturally becomes quite impossible, and at the same time quite arbitrary, for in the apparatus of movement are included two such different systems as the bones and the muscles (passive and active movement apparatus). Such limits are altogether arbitrary. For does not the nervous system which supplies the stimulus for movement, as well as the brain and nerve-fibre paths, belong here too? Are the blood-vessels to be excluded? Is the respiratory apparatus to be limited only to those parts immediately subserving the gaseous exchange, or does it include the surrounding skeletal parts and the muscles which move the thorax? One sees that by maintaining the conception of apparatus the path is trodden which leads back to Haller's physiology.

In an anatomical sense it is better to speak of system rather than of apparatus. There are features derived from anatomy, from genetics, and from comparative anatomy which define the extent of a system.

Anatomical features, since all parts of a system possess a common underlying structure in their finer elements (the skeletal system, the predominance of the structure of bone ; in the alimentary system, the possession of an internal surface) ; genetically, since developmentally all parts of a system arise from a general less differentiated primitive material, and on comparative anatomical grounds, since a well differentiated system in man may correspond to a less differentiated system in a lower animal, and even may correspond to a single organ (for example, the whole axial skeleton corresponds to the notochord). These furnish definite limits ; they also furnish the criteria for the place of an organ in a particular system. The mammary gland belongs to the ectodermal system, both on genetic and comparative anatomical grounds, however strongly its function claims alliance with the reproductive organs. There is of course a urinary apparatus and a genital apparatus, but there is only a urogenital system, since these have in part a common developmental origin. The thyroid, the parathyroids, and the thymus do not belong to the masticatory apparatus nor to the internal secretory apparatus, but to the alimentary system since they are developed from this. It is wrong to separate a bony system from a system of joints and ligaments (as is done in many textbooks), since cartilage, bone, joints, and ligaments arise from a common primordium, and there is therefore only a single skeletal system.

We have now by these tests a better means of classifying the body based on distinctive anatomical features than had the anatomists of a hundred years ago. Despite the value of much in the work of that time, we cannot help seeing how vague were their anatomical boundaries.

Let the beginner direct his special attention to the application of these boundaries in those systems in which a tissue element is preponderant. Skeletal and muscular systems consist of organs, the bones and muscles. Each bone and muscle is to be regarded as an organ. According to the above definitions, the functional value presents a well-marked distinction between bone and kidney, but tells us nothing in respect to their form value. Besides, numerous tissues go to make up the bone and also the kidney. Although in bone the bony tissues predominate, yet is the bone more than bone tissue; its growth, its nutrition, its reactions, depend on a multiplicity of tissues. We have to be on our guard against this misleading confusion of the distinction between organs and tissues.

We feel that this argument is not merely a question of words. Its importance is enshrined in the following proverb. The apparently small things affect also the great things, and vitally so, if we recall what lies at the basis of all good teaching, "*Qui bene distinguit bene docet*"—(*et discit !*).

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General Part.

Life, its Essence, its Evaluation, General Morphology, and Ætiology.

Para. 13. This general part will concern itself with the appreciation of those considerations which we have described as fundamental, the morphological and the ætiological. It is necessary to show now that they are fundamental. Both considerations can be applied to the whole of nature. If anatomy were not a science of something living, then all morphology would end in stereometry and all ætiology in mechanics. This is possible in the inorganic sciences; since the reduction of energy and matter to the amount of work done measured in absolute units is possible, space and time can be excluded, and everything expressed in terms of the work done. As the irreducible residuum there remains only the arrangement of the material units in terms of their electric charges (Häring). It is otherwise in the living. Here there remains an important irreducible residuum which is life itself. Morphology and ætiology are therefore nothing more than stereometry and mechanics applied to life. Stereometry is to be understood in its widest sense; since we might conceive of the possibility of reducing the form of the organism and its organs to a formula, and of thus instituting comparisons of an exact nature. But nowhere at the moment is such a possibility visible. In its place to-day stands what is known as promorphology [para. 48]. Life cannot yet be regarded as a sort of arithmetical remainder which one can ignore as if it did not exist in order to reduce the rest to scientific terms. This remainder, life, intrudes into every investigation carried out on the living, because organic forms possess three features which are the immediate expression of life—their internal complicated form (organization), their individual form (individuality), and the purposeful character of their behaviour. Since all three features of the living organism enter into every consideration, morphological and ætiological, it is necessary to hold clear ideas on the objectivation of life. This again demands an insight into the essence of life. Before we enter on the consideration of general morphology and ætiology it is essential to investigate life itself in the light of the two conceptions already mentioned, i.e., what we mean by life and how we are able to apply the conception objectively.

(I) The Conception and the Objectivation of Life.

(A) The Conception of Life.

What being alive is we know only from our own sensations. Our conception of life arises solely from the fact that we ourselves are alive. When we form other conceptions we do so by abstraction and determination. But the conception of life is sharply distinguished from those conceptions which we reach by logical thought. There is here no superconception under which we can arrange life, nor are there similar conceptions from which it can be separated. There is only one definition—life is that which we feel, or life is that which we recognize working in ourselves, or quite briefly, life is life. The conception of life has then no satisfactory objective validity (non-constitutional, Kant), but only an idea leading to a correct judgment of things (regulative, Kant). Therefore there arises in nature the impossibility of sharply defining the limits of life. This would only be possible if life were entirely an objective phenomenon. There are then for us no certain boundaries between the living and the non-living and the dead (two ideas wrongly linked together as being of the same significance). In both cases we may fall into the error of believing that something which is actually alive is non-living or dead, since it does not show the signs which we associate with life (a resting seed, a cold-stiff animal, and an apparently dead).

On the other hand we might ascribe life to what is not alive, as, for example, a flame (Roux), or to a whirlpool which always retained the same form, by attributing to it the same feelings as we ourselves feel.

In all this it is easy to show that we commit the logical error, *petitio principii*, that is of using what is not proven as a means of proof. How can we determine objectively that something lives when we only comprehend life subjectively?

This apparent error marks, however, a definite step in the knowledge of life, the only step which is possible at all. Since only if we join the conception of life, it may be in itself as it will, to other conceptions to form a judgment do we arrive at an objective scientific conception of life. We, therefore, collect and assemble what we regard as the manifestations of life and declare these shall be used as tests of life; anything which does not show, and never has shown, these manifestations is without life, and further, that which has shown them but no longer does so is dead.

Many such objective features of life have been gathered. Complicated form, absence of reproduction, growth, and of assimilation, have been brought forward as distinctions between the non-living and the living; yet it may be shown that some unicellular organisms possess a simple stereometric form (radiolaria), while growth and regeneration occur in non-living structures such as crystals (Rauber). With the metabolism of life may be compared processes in the inorganic world as, for example, the flame (Roux), and carbon dioxide production in lead chambers. In the inorganic world there can be found imitations of movements, growth, and division (Roux). The boundaries between the living and the non-living become equally obscure when we depend on some such criterion as metabolism movement, or reaction to stimulus. For apparent death, sporing, hibernation, rigor mortis surrender life fully, but yet may retain the potentiality of life and still possess the *vita minima.*

The characters of life are defective in all these, but they are not actually dead. They form a particular link between life and death. Also death and life can exist simultaneously, since an animal does not die in all its parts at the same time (details in Verworn). There is thus no one feature which characterizes life objectively, but rather a group including some which are found in the apparently dead, but never in the actually dead.

According to the scheme of Roux, life can be defined by nine functions and two principles. These nine functions are dissimilation, absorption, assimilation, excretion, growth, movement, reproduction, inheritance, development. These must all be present if we wish to speak of life. This number of characters is satisfactory only for the moment, for it is possible to assume that some of them may prove to be combinations of others, or fresh ones may have to be added as the result of new observations. These nine functions are subordinated to the two principles. The first and chief is that the living organism can carry out these functions itself (therefore it is auto-dissimilatory, auto-receptive). We may therefore describe the living organism as self-working. Further, the living organism is so conditioned as to influence these various functions in such a way that under normal conditions, and within a fairly wide range, under abnormal conditions the undisturbed maintenance of the whole results. The organism therefore possesses the capacity of self regulation.

"Self" in this connection signifies that the factor for self-governance lies in the organism itself, and there affects the influences from outside. That self-working and self-regulation are only names incorporating the conception of life, and of course of a purposeful life, scarcely needs mentioning.

The whole nine functions and both principles must be joined together if we are to ascribe life to something. Accordingly the pre-scientific conception of life has become a scientific judgment on life. Since all these nine functions bring about changes, and according to the principle of self-working these changes must take origin in the self of the living organism, we are confronted with a new idea in this notion of self-regulation. These functions determine the change (metabolic, form, energy change), while the self-regulation maintains permanence in all changes. We are now confronted already with the fundamental distinction of the behaviour of the living organism. For the change consists in the regular sequence of alterations; it is under the dominance of causality. Permanence rests on this, that the whole of the changes leave the form untouched. Organic growth is only rational when it does not destroy the form: reproduction, development, heredity, are included in this statement; the forms are unchanged if we make the time factor large.

Permanence and change identify themselves with the old problem of being and becoming, which have always possessed a great importance not only in philosophy (Simmel), but also have strongly influenced the whole attitude of mankind to itself. (Is there a progressive development of the human race? Does the world become better? Is there any progress? etc.—Grützmacher). In philosophy there are systems of being (for example, Eleatic, Plato, Schopenhauer) and systems of becoming (Heraclitus, Hegel). Being and becoming are often regarded as contradictory states of which only one can be rational. In reality, however, there are two sides of life to be apprehended which are always present at the same time. The special problem is their effect on the thing in itself, which, however, naturally does not affect the investigator.

It is the becoming which was clearly recognized in a prescientific sense. What science can add is to determine the factors governing these becomings. Insight into the state of being has always eluded the general, and also the most experienced scientific judgment almost entirely.

This insight has at all times been regarded as something very precious. How shall we understand it? Purely empirically we feel our being in consciousness; we recognize it in the similarities of various types in the working of heredity, in the agreement which prevails in many characters among allied species. Beyond empiricism the dissimilarity of one organism to another manifests also a something persistent, as the skull of man and the skull of the Selachian, the number, the course, and the position of the cranial nerves in skulls very different from one another, the same ground plan of the extremities in highly dissimilar forms. Even where there are no extremities we can find something of the fundamental [para. 66];

the alimentary tube does not arise from nothing; it is found in the Gastreæ; and before this it is part of the surface of the blastula. Embryologically the manifest complexity of the developed embryo can be referred back to a state invisible and undeveloped [neo-preformation, Roux, para 84]. Finally, this problem of being carries us back to the problem of preformation, and the derivation of all new structures. All becoming is then regarded as only the unfolding of being; [nothing appears which is not already there; what is not we cannot conceive as originating (Goethe)].

Our distinction in the criticism of life in these two ways is now well founded. The further implications, questions, methods, and results, depending on these, we will consider further later.

Para. 14. On the relation of the living whole to its parts, on the origin of life, and on the relation of form and function to one another, arise contradictory views. In the conflict of these opinions one must remember throughout that all these questions can be answered only in a mass of contradictions, since opposite standpoints will enter into the judgments and so must lead to contradiction. The contradictions have distant similarities with the antinomies of Kant, rooted perhaps in the same opposites which were significant in the antinomies. We will not so term them here, particularly since the critical basis which Kant gave them has not remained without objection. It is better to regard them as "aporien" (problems from which there is no way out) of life. There are two such "aporien" in the science of living things. The first is that of causal relationship of the whole to its parts, and the second is that of the origin of life.

In the first insoluble problem there are two assertions. The form and the changes of the organism are to be explained on the mechanism of the parts alone. On the contrary, without an influence of the whole on its parts can be explained neither the form nor the changes of the organism. The solution of this contradiction is that the whole and the parts are representations arising in space simultaneously. Since space is a continuum, infinitely divisible, so we proceed right to the end until we, in our phantasy, are postulating parts. In ordinary understanding this idea is usually so conceived that the whole is regarded as being composed of its parts. This is why the problem becomes insoluble. If we make something out of parts then the authors of the first view are correct. They are, however, still incorrect for the reason that the organism is not a composition but a continuum and a whole. If one proceeds from this integrated whole, one can with an air of correctness adopt the second view, but yet only with apparent correctness, since one neglects the continuum; that is the circumstance that the whole is not the sum of the parts, cannot be set apart, beside, or above them, but is rather a simultaneity of them all. There is no power which can be attributed to the whole, but only activity which resides in the parts, and therefore can only be observed in them, which is what the first view asserts. If one does not avoid this fundamental defect of imagining the whole to be a combination of the parts, one thus merely proceeds in a circle. If one avoids this and holds the empirical phenomena before the eyes then is one able to study, from case to case, the changes of one, few, many, and all parts, and the working of such changes on one, few, many, or all parts.

The whole is therefore excluded from all ætiological considerations. As a representation, arising at the same time along with the parts, it is the object of morphological consideration. Only as "being" is it comprehensible to science. As natural scientists we express both methods of considerations when we say form, metabolic, and energy changes are bound to a typical structure undisturbed by change.

The physiological investigator finds an immeasurable field in the investigation of metabolic, form, and energy changes. All that he discovers here he may place in a strictly causal relationship and follow experimentally the processes. He must, however, accept this fact, that without the actual cell, without its constitution of specific material, and without its obvious specific arrangement in space (though not visibly demonstrable), his investigations are without foundation. The fact that in the colloidal material of protoplasm and cell nucleus there are specific structures present, which, if destroyed, can again be demonstrated (*melacomorphosis typica et regulatoria*, Roux), brings before our eyes the most potent, and at the same time the most mysterious phenomena of life. Like the metabolic processes, so also are the form changes bound up with the processes of biophysics and biochemistry taking place in the parts. The form change is only the change of a given form and is never large, but restrained within the very narrow limits of change that arise in any given form. The stream of energy that pervades all being is the same. But none the less each of these beings is different from the others, each is typical, each employs its energy specifically and is capable of specific self-regulation. This typical structure we could explain causally only if we were able to trace this structure back to its historically older but equally typical form.

In the second insoluble problem it is asserted, firstly, that life had an origin (principle of origin); secondly, that there is no origin, but all life is derived only from other life. The explanation of this contradiction is to be found in the application of the law of causality to the irrational idea of life and its objectivations. The law of causality demands for every state an earlier state, upon the alteration of which the later state follows. Life is, however, not a state which is purely objectively determinable; it is at the same time the expression of something subjective, and the application of causality to life leads tc insoluble difficulties and insuperable contradictions.

Only when one excludes from the conception of life and its objectivity the subjective element can one accept a non-living state which is applicable to the living. It is the ætiological attitude of physiology again that renders such an exclusion unthinkable. For it there are no living organisms (cells) but only living substance. This is in itself futile, since life is apprehended only in the feeling of living, and this presupposes a "self," not a "substance." Since, however, the question of the establishment of life is scientifically justified so the ætiological investigation must take hold of living substance in order to have a starting point. It is sufficient for it to accept a stabilized system of definite developmental capacity (Jensen) as a starting point for later organization. The evolutionary theory of the weeding out of the unfit derived from the philosophy of Darwinism is seized on in order to render comprehensible the gradual increase of complexity of the system.

If, on the contrary, we do not exclude this subjective self-consciousness of life from our conception of life, then such a conception stands and falls with the living, formed, individul organism. We have again co-ordinated the ætiological considerations with the morphological. It is in this only that the law has any value —that life is derived from life (*omne vivum ex ovo*). In this case the achievement of organization and individuality from non-organized and non-individualized would signify that each subjective character can arise spontaneously in us. From this point of view, therefore, we may decline to accept the doctrine of the transmission of life from life. The classical expression of this derivation was reached in the law of Virchow—*omnis cellula e cellula*, and its expansion into *omnis nucleus e nucleo*. Moreover, the teaching extends still further to the continuity of specific tissues (cartilage from cartilage), and finally, in the mosaic theory of protoplasm, the doctrine of the organ-forming germinal areas and paths [para. 90 ff].

The obvious difficulty which confronts the doctrine of *omnis cellula e cellula*, is this, that the existence of cells organized, as we now understand them to be, from colloidal masses must have been difficult at the time when the earth was in the state of a fiery, fluid mass. The only help is now either the extension of the ideas of organization and individuality to the cosmos itself (cosmic organization, Fechner; and quite recently, Bolk), or the extension of the conception of life to all inorganic material (Preyer).

Fechner has extended, with his idea of the cosmic organism, the conception of life to the whole world and regards the entire universe as a parent organism, the essence of which consists in the indissoluble relations of all the individual phenomena to one another. The present would therefore show life in such a relation, but no longer in the original condition. Some modicum of truth lies herein. The harmonious adaptation of one individual to another (male and female, animal and plant, flesh and insect feeder), and the obvious functioning automatic self-regulation of the entire cosmos in the maintenance of these relations, proves the presence of a super-individual unity and organization. However, we can make no representation of such a being, and therefore it lies outside the range of scientific investigation. Philosophically, there can be no objection to such a view, since it starts from an ascertainable judgment of life, which, of course, differs from that of natural science, but is throughout tenable.

In the same manner Preyer desires to look on the organized as the ancestral form from which has arisen during the cooling of the earth the "no longer organized." If we can form no idea of the nature of any such original state it is not beyond the range of possibility, and would render intelligible the "probionts" as forms of life sunk in the inorganic world. Yet the origin of organization and individuality remains unexplained, as it does also in the monism of Haeckel. This is the case with all attempts at an explanation of origins. Noteworthy is the recent pronouncement of Roux, who, using the principle of selection, starts from the fact that there are present outside the living world systems which in part express some of the features of living things, particularly assimilation (flame). Hence he has applied to these the name of "like formers," "isoplassonts" (Roux). If these are followed theoretically by the development of more complicated forms ("self-movers,"—autokineonts; "self-dividers"—automerizonts; "self-inheritors"—heridonts) as steps towards the establishment of living forms, under the influence of natural selection, and if their artificial generation is conceivable—without reference to its actuality—so does the step from "probionts" to "bionts" include the acquisition of organization and individuality, against which valid fundamental objections are directed. The causal and morphological views on the origin of life are at the moment irreconcilable.

We now direct attention to a third question, which is contradictorily answered. This is not an "aporie," but rather a case of simple inexactitude. It is this: Does form govern function or the reverse? The logical error of the question is that here there are not two things bound together in a causal relationship, which alone is valid, but rather two views which we have of the same organism. One can as little explain function and form by one another as the tone of musical score by its rhythm. We are of course not referring to the relationship between form and function in a particular individual organism. In such a case we are concerned only with the investigation of sequences, and so one meets with many relationships between form and function. There are forms without function (non-functional period in development [Roux] produced only through heredity) ; there are mutable forms (forms dependent on function, functional adaptations), and functions made possible through the emergence of new forms (functional changes, for example, the placoid organ of the selachian being transformed to teeth as soon as these organs arise in the mucous membrane of the mouth). However, all these are only possible in special highly developed relationships of a causal type and only arise in so far as a form is unfolded, and a function is present simultaneously. There has never been a form without function, or a function without form. In practice one can explain form in terms of function (the form of the heart through the bloodstream, the form of the teeth from the mode of nutrition), but only in so far as the phenomenon in question begets the succeeding phenomenon. The existence of these phenomena, as, for example, the cartilages of the larynx, the twisted heart tube, the placoid organ, is functionally not further explainable. Similarly, one can derive the function from the form (the joint movement from the form of the joint, the flow of the blood from the form of the heart). These, like the above examples, are ultimately only different ways of describing facts teleologically considered.

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(B) Objectivations of Life.
(Organization, Individuality, Purpose.)

(1) Organisation.

Para. 15. The three ideas presented here have already been described as objective features of all living things. They have therefore to take their place in our systematic account of this point as a premise of what follows. The first two have this quality in common, that they are incapable of any logical definition. They are as little objective as life itself (constitutive ideas, see p. 34). They are not subordinate to other ideas, and they have no limiting value. They are therefore irrational, that is they cannot be circumscribed by any logical process. Of purpose, we can quite well give a clear definition since we are familiar with technical apparatus suitable to its purpose (the agreement between form and determination); the irrationality first appears here when we transfer this definition to the evaluation of life itself.

We proceed to an investigation of the problems of organization. Any definition attempted here must bring a discussion of organization, as for example this: "An organism is an integrated collection of parts which stand in reciprocal relation to one another and alternate as object and means." Quite apart from the fact that the body is not a collection, the relations in the organism between the whole and its parts cannot be expressed in words. Exactly in these relationships lies the irrationality of the conception of organization. The irrationality is threefold (genetic, formal and causal).

The genetic error consists in the following: We see an organism composed of parts, and at once conclude that the organism is a collection of parts. Yet a process as that of combination is nowhere demonstrable and certainly not during development. One part never becomes added to another, as in an aggregate or in the formation of a crystal, but the whole and the parts exist at the same time at every stage. "The whole forms the parts," and distributes itself among them. The formal irrationality consists in the following: It is an abstraction alone that sees the organs of a body as relations in an organism. They are, however, only demonstrable and preparable as individual structures. So there arises a contradiction between what the anatomical material is as a study and what it is as the object of our thought. An object, "brain," cannot be considered like an object, "fly-wheel," of a machine. The latter has a meaning in itself, but the former has none. Everywhere the severed vessels and nerves of an isolated brain show its continuity with the body. If we were able to imagine that no animal form was known so would the brain appear to us as so much debris. This also reveals to us the senselessness of anatomy confined to the cadaver [para. 10]. The causal irrationality consists in the following: The phenomena of life are referred back to the parts of the living organism itself. Each part exerts its influence on the whole. Despite this the activity of individual organs appear to be regulated through a radiating influence of the whole. (Harmony of all growth, all metabolism and organ formation, e.g., maintenance of the proportion of all parts, times of ossification, p. 141.) Finally, each part is conceived as the actual cause of the activity of every other part (for example, correlation, the function of the visual organs, co-ordinated muscular movement, body movement, normal circulation, nutrition of the eye).

The question now is what can we scientifically, and therefore also as the result of experience, assert about organisms? Embryology allows us to state that originally the whole and the parts are one (the fertilized egg) and that the entity at first exhibits few and then later many parts. An entity apart from its part does not exist.

Formally we can only demonstrate that there is a form equipped with an entity-formed member, an unity bound together in a continuum by connective tissue, nerves, and blood-vessels, smooth and striped muscle, which we can artificially dissect into parts (organs and cells). There is no causal relationship between two organs, since there is no significant temporal relationship between two changes but rather the change in an organ, which we might regard as the consequence of a previous change in some other organ, must be again the cause of the change in the first organ (e.g., the heart supplies the nutrition of the medulla, but the function of the heart depends on the activity of the medulla). The fact that an isolated heart beats does not contradict this since in normal life the automatic centres of the heart are not in control. In a similar manner the causal relationship between a part and the remainder and between the whole and the parts rests on what we have already stated above. The words, often now much used, "entity, integration," are fashionable catch phrases. One must hesitate to use them when discussing questions of ætiology.

Traces of an integrative activity have often been supposedly found, e.g., in the activity of the presence of the metabolic products of the ductless glands. It is proved, for example, that the deprivation of the thyroid excretion destroys the correlated development of the frog larva; the proportions of the body are regarded as due to the activity of the hypophysis. Nevertheless, one cannot speak of this as the activity of an entity, since this is only a question of the activity of the hypophysis or of the thyroid gland which, in their turn in the normal body, are under the influence of the nerves, blood-vessels, respiration, metabolism and the sexual function. It is also very possible that all organs furnish an internal secretion to the blood. The relation of the parts to one another would only become more complicated by this, but it would be an error to hold the effects of universally distributed metabolic products of an organ for the effects "of the whole." One could then—and this appears often—accept a psychical factor such as the will as a determinant issuing from the whole. Either this may be an immaterial factor (entelechy, determinant, dominant) which would not be then available for investigation; or it may be material as the working of an energy; then the above laws would be valid and applicable to it; then it would be localized at one point, such as the brain, and therefore dependent on the nutritive supply, or it would be actually in some organ, and therefore dependent on this for its metabolic changes.

Dynamic influences which start from a centre and exert a widespread influence actually seem to be present. Perhaps each cell division is to be looked on as a dynamic process streaming out into the surrounding substance, and through the influence of its activity calling forth other cell divisions [Gurwitsch, para. 107]. Still more wonderful seems the fact that at the time of gastrulation in the frog larva there appears a cell complex which arouses a developmental stimulus, not only in the surrounding substance, but also qualitatively influences their formative properties while it itself appears for the most part to be independent of its surroundings. If one removes such an organizator of a frog larva from the mother substance to the gastrula of the triton larva, then under its formative influence the triton material acquires the pattern of the frog's tissues and organs (Spemann and Mangold). How to understand these facts rightly is not easy, since the dominating cell divisions must be affected themselves, and it appears to hold, e.g., of the organizers, that they can be influenced by the organism, and those parts which were originally dependent upon the organizers can later be transformed into organizers (Spemann, 1921). Irrational substitutive changes appearing as typical for organization cannot therefore be excluded.

In summary it is possible to say that the immediate morphoogical objects of knowledge can only be the form of the whole, its members, the form of the parts when artificially separated from the assemblage, and the manner in which they are apparently linked together.

Our knowledge becomes the more and more certain the less we are obliged to tear the organism asunder. In fact, the ideal is the investigation of the living. Ætiologically the study of the organism only reveals between the steps of causation fragmentary links, and these, as such, can only be relatively independently recognized. The determination of the true cause of form must proceed by other paths [para. 32-35].

With the preceding also arises the question of the value of organs. Value presupposes some standard for measuring it. This can be selected morphologically or physiologically. Necessity is the best measure of value. One might speak in the first place of organs necessary to life. An organ can be called vital when its defect leads to death. The number of such organs is not large, since primitive animals can survive without brain or spinal cord. In respect to man things are naturally otherwise. We can also speak of vital necessity in regard to man, meaning those organs which furnish the optimum life value. Here it may at once be questionable if unpretentious organs such as nails, hair, wool, rudimentary organs (vermiform appendix), organs of obscure significance, like the tonsils, have not a value. Necessity has a third significance: that there is, if the organization of vertebrates is taken for granted, no superfluous part, since all differentiation arises necessarily from the primordium which originated in the inconceivably remote past. We have to apply this morphological necessity as a measure in evaluating the organs of our body. Not in what way the organs serve the body, but in what relation they stand to the primordium is the question. From this standpoint, if we ask what is the value of hair, or nails, then the objects of the comparative anatomy of man stand in full view before us.

Para 16. We make a considerable use of such evaluation when we come to talk about higher and lower organization.

When we compare adult organisms with one another we learn, e.g., that there are beings in which the stomach and intestines consist of a simple cavity, the heart of an undivided tube, or such in which the skull consists of a cartilaginous capsule fitted like a cast. We recognize organs of smell which persist throughout life without glands; an auditory organ whose cochlea is represented by a short, blind sac. Through the comparison of the various degrees of organization of organs and from the study of embryology one arrives at the idea that the inner complexity of organization rests on a subdivision of work essential to the organism (division of labour). The rich complication of more simple primitive organs produces a state in which at the same time the new co-ordinated secondary organs subordinated to the primitive and taking its place are distinguished from one another in structure (differentiation). One can thus describe the establishment of organization as the formation of the differentiated out of the indifferent, wherein we should make no distinction between the apparently indifferent, but with as yet invisible numerous potentialities, and that which is indeed indifferent from both points of view [para. 84].

The relation of division of labour to differentiation is to be judged as similar to that between form and function. We do not know whether the division of labour precedes the differentiation or vice versa. Differentiation may be foreshadowed, for example, in the greater complexity of the germ. The "work" would be only the releasing moment; the division of labour the consequence. In the adult organism it appears, on the contrary, as if the use preceded the differentiation. Therefore here also it is best to speak as if there were only a parallelism between the division of labour and differentiation.

This conception we now use for determining the level of the organization. We regard a low organism as one in which division of labour and organization are wanting and a higher organism as one in which these are carried to a higher degree of development. An organism which possesses a straight intestinal canal is in this feature more primitive than one which possesses a canal coiled many times and divided into stomach, mid- and hind-gut, with differentiated epithelium and provided with specialized glands and epithelial thickenings. Lower organisms have a segmented kidney opening into the cœlom; higher, a kidney which has lost its connection with the cœlom and is instead a highly complex organ with ureter and bladder. The association of bladder and reproductive organs, of hind-gut and cloaca, is primitive; higher is the separation of the male genital glands from the urinary system and the division of the cloaca into hind-gut and urogenital sinus.

In all this there are present uniform fixed ideas, whereby, using the terminology of morphology, the selachian is more primitive than the reptile and the monotreme more primitive than the marsupial. The total comparison of the organization results in the classification of the vertebrates in an ascending series; this is often mistaken by physiologists, zoologists and even by anatomists; for it implies no contradiction to the principle that a fish may be as perfectly organized as man and that, therefore, there are no lower or higher forms. This is quite correct. The behaviour, in opposition to the principles of morphology, is made the test, in place of the degree of differentiation, only from the latter is derived the judgment of high and low which have nothing to do with value of behaviour. On the contrary, it follows from the conception of the division of labour that the value of the whole behaviour must always remain the same since it is only concerned with the preservation of the individual and the race. The statement that all organizations, if one values the whole in reference to existence, response, and vital needs of the animal, are equally perfect, is without any scientific value since it only describes a truism.

If we would give a definite value, from the functional standpoint, to the various organizations we must employ the ideas of complication (Gegenbauer) and explication by affirming that, measured by behaviour, those animals are highest which exhibit the most complicated response with fewest organs. That which stands lowest would accordingly have to carry out physiologically the most complicated behaviour which follows at once from the principle of the division of labour. The amœba possesses the most complex body, since in the same protoplasm it has to carry out the most heterogeneous processes, such as metabolic exchange, stimulus, reception, conduction, movement, etc. The differentiated type possesses special organs for carrying out these various processes. Even in the highest forms seldom has one organ only one special function. If explication advances with ascending differentiation it is also true that in the higher forms there is still enough of complication.

Among forms standing on an equal level the absolute value of behaviour can then form a test of classification. One can then speak of more specialized and generalized systems, organs, etc. The eye of the bird, the olfactory organ of the fish or carnivore, the stomach of the ruminant, are all specialized organs capable of a high level of achievement. The organization of man is distinguished from that of all other animals in that his organs, with the exception of the brain and the extremities, are marked by an average level of performance, without one-sided specialization, so that they are capable of a more general excellence.

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(2) Individuality.

Para. 17. This conception also plays an important rôle in anatomy. In spite of all that has been written about it the verdict as to this fundamental conception of the science of the living is quite uncertain. The whole question of the being and significance of the individual is still for natural science in the "prescientific" stage, from which the judgment is delivered that individuals (indivisibles) exist. These none the less can be divided, and it is therefore not possible to grasp the essential nature of individuality. The most striking points, which can be stated purely empirically, are contained in the Haekelian distinctions between anatomical and physiological, actual and virtual, individuals. Those individuals which really exist are actual, those portions of them capable of forming a new individual are virtual.

Meanwhile, not only have the facts materially increased, but the question as to what the individual is has proved itself of importance not least with regard to medicine (Kraus) and to anatomy (Lubosch). It is further not yet by any means clear how far we may expand the conception of individuality: Is it to include animals, plants, cells? Is it an essential conception for natural science at all?

In the first place the phenomena of the individual must conform to absolute simultaneity. For this reason, if for no other, every intellectual concept of the individual (not of individuality) is impossible, since as the immediate object of observation it at once loses its simultaneity at each subordination. For the same reason, it is not identical with "organism" and "whole," for both of these, even if no objective conception of them can be found [para. 15], are conceived as divisible into species. Every individual is admittedly an organism, a whole; the question is whether every organism, every whole, is also an individual. Before we can be satisfied that we have an individual, we must always have something further of a particular nature; objectively this is simultaneity, subjectively it is consciousness of the ego. Individuality is accordingly the objective phenomenon of a being conscious of itself as ego. At the objective phenomena of individuality we shall look more closely later, for the moment they may be passed by. The subjective phenomena are psychological, and can only be immediately determined by each one of us in his own case. Man is conscious of himself as an ego; he possesses the feeling of freedom and responsibility; he feels himself a moral being. To this must be added his feeling of the unity of his own life, the conception of his indivisible body; he holds sway over his own conceptions, forms within himself an "inner picture" of himself, and calls forth an "outer picture" of himself in others. From these and certain other characteristics we gain the conviction that each of us is an individual, and upon that we base the right to our conception of the individual, for man at any rate, upon a firm foundation (Müller-Freienfels). These psychological observations of self are no more than observations of a set of circumstances (*individualitas individuata*), which certainly form a guarantee of individuality, but which do not themselves form the essence of individuality. The actually observing, judgment-forming ego (the *individualitas individuans* is not immanent, but transcendental. With Schopenhauer, we see therein the will, the "thing in itself," which only attains to consciousness of itself in the objectivation of an individual being. According to Schopenhauer, individuality is the immediate representation which I have of myself when I perceive myself simultaneously as represented object and representing subject. This leads at once to the further conclusion that individuality must be a property of all human beings at any rate, since otherwise the individual would necessarily regard himself as such, but all others as beingless schemes (Schopenhauer).

Whether and to what extent we are entitled to ascribe such an ego-consciousness to animals is a question which may here be left unanswered. Observation of the higher animals, however, gives a considerable measure of justification for the assumption. The specifically human increase in this consciousness of the ego, until it reaches the degree of a being conscious of itself, morally responsible and free, may be designated by the idea of the "person" (Kraus). In this way obliteration of the boundary between human and non-human individuality is avoided, and we are then at liberty, relying on the objective characteristics of individuality, to go to the extent of attributing this quality to animals and even to cells, particularly in so far as these possess something analogous to the nervous system and the sense organs, since it is with these organs that our own power of observation and self-observation is most intimately connected. In any case there can be no certainty. We have constantly to keep before us the fact that the salient feature of individuality is a subjective one. It is inseparable from the indivisible entity which attains to the idea of itself in every objectivation of the will, but which can do this only when the objectivation takes place in matter. By this means a path is opened towards an understanding of that which is irrational in the idea and the word individual. Irrational is, in the first place, the subjective phenomenon of the individual to our self-observation. For, though it is true that we feel ourselves the same throughout our whole lives, yet it is equally clear that at different times we feel and judge ourselves and others feel and judge us as different; that we act differently, and in a way which does not correspond to our individuality, and even fail to act or to be recognized as that which we really are. Our bodies undergo constant change, not to mention the transformation or destruction of individual consciousness in the case of mental diseases (Müller-Freienfels).

Far more striking is the objective irrationality of the individual which has always been emphasized. It is here that the main difficulties lie in determining what an individual is. It has long been recognized as a fact that organisms are divisible, and that the term individual, applied objectively, is therefore inapplicable in this case. Paramecia, hydras, worms, ascidians, are divisible into fragments which again form entire creatures. There is no need, however, to refer to artificial division; every cell-division, every germination, as well as parthenogenetic propagation, shows us the dividing of an individual into two. This is even true of the organs, hitherto regarded as morphological individuals (E. Haeckel). In the case of many of them (glands, taste-buds, intestinal villi), M. Heidenhain has shown that they are part bodies, i.e., capable of origination through a sprouting. In the case of the organs of the sense of touch and the hair this fact was already known. Of great significance for the problem of individuality is the behaviour of segmenting germ cells, since two, four, or eight embryos may result from the fertilized egg intended for one individual, if the 2-8 first segmenting cells are developed in isolation from one another [para. 87]. Physiologically the same process appears to take place in the spontaneous formation of twins from a single fertilized ovum in mammals [Sobotta, paras. 82, 83]. A. Rauber attributed this to a doubling of the primordium. Of unsolved origin is the fact that in the armadillos four or even eight embryos are produced normally from a single fertilized ovum (polyembryony, Fernandez). Rauber therefore called attention to the fact that double monsters and the production of several young from one ovum justify us in regarding the vertebrates too as a kind of " colony " (Cormus). In any case the eight vertebrate embryos which derive from one ovum are a true colony formation, such as otherwise occurs only among invertebrates (polyp-colony).

Light of a different kind is thrown upon the question of individuality by the opposite process, viz., that by which a single individual may result from the primordium intended for two individuals by the union either of two ova (amphioxus, Strasse), or the first two segmentation cells into a single four-cell stage (triton, Spemann). In this case it is perfectly clear that individuality is not referable to any material basis. E. Haeckel's old notions of virtual and actual individuals (see above p. 48) may be applied to these cases too, for virtual and actual individuals must be distinguished here even when the actual individual is not converted into a virtual one by artificial means. Every primordium must then be described as pluri-individual, and in particular is this true of man (facultatively, virtually pluri-individual) and of the armadillos (typically, virtually pluri-individual) while the fact of actuality must be made dependent upon failure of the primordium to divide.

After the purely morphological, mention must be made of the genetic irrationality of individuals. Embryology also resolves the individual, since, going back to the germ plasm of the fertilized egg, it regards the constituents of the latter, the genes, as in a high degree independent elements, which, in the formation of a new individual, separate from one another and meet anew in a variety of combinations. Accordingly individuals are merely new combinations of material elements limited in time and space. A purely dynamic consideration leads to the same results, since this shows that the forces at work in individuals are in no wise specifically individual, but are similarly a series of forces combined in space and time to form a system in a state of "preparedness for work" (Kraus). Here, too, of course the "individual matter" arising from this union must not be lost sight of (Pfeffer, Löhner); this is of importance for amphimixis, since it hinders the union of individually closely related organisms.

All this shows that the individual, regarded purely empirically and materially, remains entirely irrational. It is for human anatomy in particular that we are faced by the burning question: What is the individual into the structure of which we endeavour to penetrate in the laboratory? Is it nothing but a combination of characteristics which, alternating about a mean, would produce in another combination another similar individual? The same question faces us in histology and in embryology. What are these elementary individuals, the cells? What is the fertilized ovum which we study under the microscope? Are they aggregates of qualitatively differing elementary parts combining in numerous ways? We reply that they are, firstly, organisms [para. 15], and secondly, at least as far as man is concerned, an ego, i.e., objectivations of the living, beyond which experience is not able to express any further opinion. Individuality, just as little as organization, is a purely objective idea; it is entirely regulative. It is in the nature of things that the intrusion of the transcendental into the world of phenomena should be so noticeable in the object where one believes that one is peculiarly able to apprehend objectively. This applies above all to the object of anatomical study, the human individual. Many questions here arise. Does the ego-consciousness originate in the object, as monism demands? Or does it originate in thought, as in the dualistic theory? Is it a parallelism between the material and the spiritual? In that case would it not follow that in generation, in the formation of twins from a single egg, in regeneration, etc., a new formation of egos must occur? [Cf. the old patristic and scholastic ideas of a traductionism (migration of souls) or creationism (new creation of the soul.)] Schopenhauer teaches that the will is present in everything simultaneously and undivided, recognizing itself in the light of the intellect. This seems to us the only answer to questions as to the origin of the ego. Research does not, however, concern itself with this, but only with that which is given. Our task is the investigation not of life—such a task would be impossible—but of its phenomena, one of the most important of which is that there are individuals.

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(3) Suitability to Purpose.

Para. 18. Organization and individuality, as a relation in space and time of living objects, are given us immediately in our perception, causality [paras. 4, 21] as the judgment a priori on the necessity of the combination of two changes in the object is given us immediately in the intellect. From observation of the living we cannot get rid of them in thought; we leave aside the subjective element inherent in them; because we are the perceiving subjects, therefore organization, individuality and the necessity of every occurrence are objective realities. To common thought suitability is also something objectively real, and appears likewise to belong to things as they are. That this is not the case appears at once from the thought-experiment by which we can get rid of it by thought; indeed we need not even do this, since unsuitabilities exist. Suitability is therefore not a fundamental objective principle for the possibility of collecting knowledge of the living. We can study no science of life without coming into contact with organism, individuals and the necessity of a cause to produce an effect. But we can acquire exhaustive knowledge of organisms without paying scientific regard to the fact that organisms possess a suitable structure. Something of key significance would admittedly be lacking if we neglected this fact. For the knowledge of organisms which we had gained would be an empty one if we were unable to show for what purpose the organs are present; we should be unable to explain either to ourselves or to others the connection of all the facts noted with regard to the structure of a living being if we failed to describe the value of one organ for another and for the whole organism, and the value of the whole for the single organs. In the inorganic world this is not generally necessary, although here too (e.g., in the lead chamber process of obtaining sulphuric acid) suitable changes take place; in the organic world on the other hand no organization can be understood if no regard is paid to suitability. Here a number of questions arise, into the discussion of which we cannot now enter. The matter falls into two parts, one descriptive (word significance, limits, phenomena of suitability), and the other critical, concerned first and foremost with the possibility of explaining suitability.

In this connection it is as well to explain clearly the meaning of the words used (E. Becher). "Suitability" can be interpreted in a narrower or in a wider sense; in its wider sense it signifies suitability of the body to meet the demands of life, suitability of the organs to perform the tasks imposed upon them (the gut for digestion, the vessel wall for the circulation of the blood, etc.). In this sense, suitability is identical with capability of life and may be termed "primary suitability." In the narrower sense, suitability signifies a relationship of a complicated nature producing the impression of some brain arranging the relation of the parts to one another. This relationship, subject to the above limitations, is found objectively in nature. We merely state facts when we describe this relationship (Driesch's "static"-teleology). The expression "purpose" must not be confused with "suitability to purpose"; purpose exists only in ourselves as the motive of our actions. We are justified in assuming its existence in all men, and in animals, as far as they are seen to perform actions with a purpose. The idea of suitability to purpose and the idea of purpose are abstractions possessing the value of general ideas in scientific investigations [para. 5].

Allusion should here be made to the agreement, from the point of view of suitability to purpose, between living beings and works of art or technical products. Such an agreement is quite justified, provided the inherent differences are not overlooked. Suitability in a work of art, from the objective standpoint, we call style; subjectively we regard a work of art which is suited to its purpose as beautiful. This agreement between our æsthetic judgment and the form of a work of art we call æsthetic truth [para. 38]. The more we feel that whatever the artist intended to express has been expressed in his work, the greater is its truth and beauty.

A machine or tool achieves its aim in proportion as its component parts contribute solely to the performance of the whole. The idea of a machine is gradually stripped by the work of successive improvers of every thing superfluous (cf. fig. 2) and is thus raised to a higher degree of suitability. The significant differences between suitability in organisms and in works of art or machines are thus unmistakable. The artist or builder is lacking in the former case unless we assume a creator as the immediate cause of the origin of organisms. Equally wanting in nature is the historical progress towards perfection, which may be seen in machines and the differences in the degree of perfection which occur in works of art; for even the most primitive organisms possess an unsurpassable degree of suitability, and while historically there is a transformation of suitability, there is no increase of it [cf. para. 16]. Further, organic suitability is infinitely more complicated than that of any machine.

Fig. 2. — Metamorphosis of the Zeppelin airship from the oldest to the latest. Gradual perfection of form, increase of suitability to purpose. (From the Frk. Kurier.)

To give examples of suitability to purpose in the human body is almost unnecessary; every system, every organ provides an illustration of it. To mention only a few of the more wonderful examples, there is the mechanism of erection (expansion of the arteries, closure of the veins by the perineal musculature incompletely (vena dorsalis penis), so that the urethra remains patent. Then the mechanism of the closure of the larynx in swallowing; the typical combination of fascia and muscles with the veins; the existence of large subcutaneous veins, so escaping muscular pressure; the penetration of the fascia bulbi by the eye muscles; the oblique penetration of the wall of the bladder by the ureters, rendering regurgitation of the urine impossible ; the close attachment of the liver contrasted with the movable situation of the uterus within the pelvic cavity and the peritoneum. As examples of a more delicate nature mention may be made of the organs which regulate the temperature of the skin (sweat glands, capillaries), the replacement of large arterial trunks by an arterial network in the neighbourhood of the joints, bone architecture and the arrangement of the fibres of the sclerotic.

Our feeling of wonder is increased if we contemplate those features which are of service not to the individual ("self-serving suitability to purpose," Becher), but to the preservation of the species ("species-serving," Becher), among which are included all those organs, and their functions, which are concerned with propagation and nurture of the young (limitations of the number of ova in the ovary, contrasted with constant fresh production of spermatozoa; self-regulation of ovulation and menstruation, development and activity of the milk glands). What may be termed interpersonal suitability is beyond our comprehension. An example of this is to be seen in the fact that abundance of glands in the skin of mammals is accompanied by a high development of the organs of smell, while birds and reptiles have a skin devoid of glands and poorly developed organs of smell. It is just as easy to say that mammals must be able to smell well in order to perceive the scent of the herd, as to assert that they distinguish strong-smelling substances because they possess good organs of smell. A similar relation exists between milk-glands and sucking apparatus (articulation of the jaw, tongue, cheeks) ; there are even features which appear to be harmful to their own organism while serving others, like the plant-galls ("other-serving" suitability, Becher). Many dysteleological features in man might be thus described as serving others, e.g., the tonsils, which provide a suitable environment for micro-organisms but thereby do harm to man. On the other hand something may be useful to man but unsuitable to micro-organisms, e.g., the acid reaction of certain secretions (vagina). This aspect throws particular light upon the purely subjective source of the proposition "suitable," since one and the same feature must be called by two directly opposite terms when looked at from the point of view of two different organisms (Petersen).

When considering suitability to purpose, we must not overlook those features which, from man's point of view, are unsuitable, if we are to form a correct judgment on the question as a whole. Frequent accidents give evidence of the unsuitability of the intersection of the air and food passages. The tonsils and Peyer's patches in the small intestine provide troublesome gateways for the entrance of the germs of disease. The attachment of the uterus facilitates misplacement and sinking of the organ. The pelvic aperture of the tube is for women a constant threat to the peritoneum; the direction of the apical bronchus and the ossification of the junction of the first rib with the sternum are among the causes of diseases of the lungs. The optic nerve lies in dangerous proximity to the mucous membrane of the ethmoidal and sphenoidal air sinuses, so easily infected by way of the nasal cavity. Finally it should be added that even so apparently perfect a feature as the organ of sight is quite imperfect from the technical point of view (Helmholtz).

Para. 19. To pursue the casuistic aspect of this question any further has no immediate value and we will therefore turn to the critical aspect. The real problems are contained in the questions: To what end, and why?

The question, to what end? is, for a representation of the organic world, a justifiable one; only by considering and answering it can we gain a feeling of certainty and of understanding. The facts that the organs of smell and the mouth must have a frontal situation at the extremity of the body, because the former exercises the function of testing the air to be breathed while the latter has to seize the food during a forward movement of the body, and that the anus must have a posterior situation because it cannot open until the digestive canal has traversed the whole of the body cavity, seem mere commonplaces. None the less they are the expression of a set of circumstances actually present and dominating the organization, which might well be different (in many of the invertebrates, the anus has a frontal situation near the mouth), but which, if different, cannot be conceived as existing in conjunction with the structure and economy of the vertebrates. No adequate description of the heart and other organs would be possible without asking questions as to the functions of the valves, why the walls of the venous capillaries in the spleen are deficient, or the reason for the existence of the glenoid ligaments? It is also of great importance for the developmental history of the body to obtain a clear answer to this question: To what end? The separate stages which comprise their development, leaving aside the causal aspect, have a "final" significance. The branchial pouches of mammals are actually "there for the purpose of" (Peter) producing the epithelial organs of the pharyngeal wall (thymus, parathyroid); the calcification of cartilage serves as preparation for the further stages of ossification; the epithelial sheath of the enamel organ helps to model the form of the teeth.

When we ask the question "Why?" in connection with these phenomena, we find a different situation. Suppose we were to interpret the purpose served by these features as their cause. This is the explanation offered by Lamarckism and by recent theories of a similar nature. Lamarck and certain of the younger investigators (e.g., Driesch, Boveri) regarded the origin of all that is "suitable to purpose" as being analogous to that of a work of art or a tool, and looked upon the need of an organ as the creative force which produced it—a theory which may be traced back to Aristotle.

In quite recent times this theory frequently appears in a veiled form when it is asserted that nature solves "constructive problems" (i.e., those which we set her); the development of bone architecture is, for example, regarded as a problem of this sort.

If this were true, then the object of development would have to be also the means of origin (the cause). We should therefore have to assume some kind of spontaneous, conscious guidance of occurrences in the organic world, involving a twofold natural science, because there would be two kinds of causality, one for the inorganic world (causality by means, Kant) and one for the organic (causality by objects, Kant). Driesch, for instance, expressly assumes such a twofold natural science.

Even if this were so, we should then have to ask in what relationship in the organic world causality and finality stand to one another. Is there no longer such a thing as causality in the original sense? Is it influenced by finality? Do both kinds of causality exist side by side?

Before we face such far-reaching results we may well see first whether suitability may not be sufficiently explained by causality.

As a matter of fact we have here an important, purely causal principle, known as that of "functional adaptation," or, better, as "functional self-formation" (Roux). This principle asserts that the activity of every organ furnishes at the same time the stimulus for its preservation; increased activity produces increased development; the direction of the stimulus leads to formative activity of the cells in this direction (formation of tendon tissue with parallel fibres). Increased subdivision endows the glands with increased surface and permits an increase in the number of secreting elements. A fragment of the small intestine subjected to the functional conditions of the large intestine is able to assume the latter's structure. In this case causal connections are actually proved, as is also the case when after the loss of one kidney the other increases in size, or when two fragments of bone unite by a callus the cancellous tissue of which is immediately adapted to the new conditions. To this category belong the finer modelling of joints, determined by heredity, through their movements, the form and branching of arteries from the circulation within them; the genesis of a parallel direction of tendon fibres under the stimulus of tension and of disposition of bone lamellæ under the stimulus of pressure; in short, all the structures of the body which are the expression of its capacity for mechanical performance. The principle has, however, a much wider field of application. For reparation and regulation in the body fall under this head too, e.g., the conversion of a club-foot into an organ of progression and of standing suited to its purpose (Pfrang), the ability of an armless man to write with his head, or to use his feet as grasping organs. It is no great step to the idea that the same rules must explain the fact that an amphibious organization, compelled to live entirely shut off from water, forced by immediate reaction to the new conditions of life to movement on land, becomes capable of resisting the drying influences of the air on its skin, and, so to speak, at one stroke assumes an amphibious organization (Roux); or that the upright posture of man can produce at once numerous adaptations (Lubosch). The old Lamarckian principle is here valid in a changed form and on a genuinely causal basis (principle of direct influence, neo-Lamarckism).

Side by side with this is a second similarly causal explanation, that of selection, as formulated by Darwin. The selection theory asserts that once suitably reacting systems exist [para. 33], the more fit survive. It can thus be maintained that those beings which, under terrestrial conditions, could not at once fulfil the vital and functional demands from within their own structure became extinct, and so we see these only as objects which once existed. We are, therefore, in a position to treat the organic world to a great extent in this respect also purely causally, and to this extent to look upon it like the organic world.

This explanation is clearly subject to certain limitations. Firstly, it presupposes that something does exist possessing an inherent "suitable" power of reaction (primary suitability, see above). If we were to assume that "everything can be capable of everything," it would be incomprehensible why new amphibia are not originated from marine creatures, new humans from non-humans constantly, or, at any rate, more frequently than is actually the case; the functional self-formation of the heart presupposes some form of heart and the existence of a definitely reacting heart musculature, that of the bones presupposes the form of the whole bone, the osteoblasts with their capacity of reaction, the antecedent structure of the cartilage and calcification at suitable points. This entire existing organization, however, up to the point at which the functions begin to play their directing, formative part, originates in the germ plasm without any influence of function [para. 32 ff]. If we imagine this non-functional development to be inherited, having originated functionally once in some ancestral form, even then the primary suitability for survival would have to be presupposed in the organism as well as the mutually suitable division of its organs. Suitability is thus ultimately inexplicable on a "causative" basis. Transformations of the suitable can alone be explained by functional adaptation and selection.

The persistence of dysteleologies in the body is also to be explained on historical grounds. This speedily becomes apparent if an attempt is made to effect improvements such as would occur to one who was familiar with their unsuitable results. It might, for example, be suggested that the air passage should be brought down from the nasal cavity as a closed tube behind the food passage. But historically the nasal cavity and the lungs have developed independently of one another. Indeed, with the amphibians the lungs appeared before any nasal cavity existed; the latter originates by being cut off from the mouth by the formation of a roof. It might be thought that the Fallopian tube might be united immediately with the ovary; but the ostium abdominale is a primitive pronephric opening. This is to be accepted as a historical event. Thus the instances of unsuitability are seen to be necessary since they go back to processes which are derived from the architectonics of the formation of any given form.

Finalism asserts that this given form is guided in its development by a vital force. This force is said to have the power of guiding the formal developmental process to a harmonious final purpose as the will of man guides his body to an action (dynamic, as opposed to static teleology, Driesch). The inability of this formative genius to abolish the ostium abdominale, the intersection of the air and food passages and the processus vermiformis deprives it at once of its omnipotence. Dynamic teleology rests in particular on the ability of the self-developing organ to carry out spontaneously definite reactions, which it has never had the opportunity of acquiring, e.g., the formation of a harmonious being from one of the two or four first segmentation cells, whose normal function is to produce only portions of the whole [para. 87 ff.], or the factors which underlie the possibility of experimentally inducing certain areas of the embryo to form organs other than those which they normally produce. The wonders of regeneration also fall under this head. The organic systems are "harmonic-equipotential" systems and are capable of explanation not on a mechanical basis, but only on the assumption of vital energy. Any such theory would be very misleading if used to explain a number of normal processes, e.g., that of ossification and bone growth, where the osteoclasts always destroy just those parts which have to be got rid of for the preservation of the form of the whole body.

Our position with regard to this very treacherous hypothesis arises, firstly, from our judgment of the facts themselves and, secondly, from considerations of a nature connected with the theory of knowledge. The impotence of the soul-with-definite-aim in the face of dysteleologies has already been mentioned. We shall look later on at the facts of the mechanics of development [para. 90 ff.], and show that it is not necessary to attempt to explain them on these lines.

Further, the explanation of the facts by the activity of some vital force brings us face to face with the fundamental difficulty of a double causality. Science cannot accept this. This vital force could only be imagined as acting in the nature of a cause, e.g., by introducing a certain constellation within a self-developing organism, from which further constellations follow; research would then have to discover a series of constellations and to place them in a causal relationship to one another. Conceived of as an act of the will, it would be a psychic act inaccessible to scientific investigation, running parallel with the facts and not entering immediately into the question as the "cause" of a form.

This leads us to decisive considerations connected with the theory of knowledge, and so brings us back to the beginning of this discussion [para. 17]. Suitability is not an independent objective fact. For it is not, like the causal principle, an objectively real principle, but rather of distinctly subjective nature in the sense that instead of rendering experience possible, as the causal principle does, it merely permits of judgment upon experience already gained. In this sense suitability is no mere "apparent problem" (Becher), for our judgment of an organism as suitable is no mere appearance. But it becomes an apparent problem as soon as we give objective existence to what has been read into nature by our judgment and then, making the full circle, endeavour to give a causal explanation of it. Then we are looking upon an appearance as a problem, whereas the appearance, kept as such, can provide us not with an explanation, but at least with a key to the understanding of the circumstances. The circumstances are commonly represented that "suitability originates in our minds" and that we attribute to organisms functions aiming at a purpose of the same type as our own motivated action. This theory, compared with Kant's, has the disadvantage that it fails to explain why man behaves as he does. Kant explains this by leaving us a choice between two possibilities only. We may have causality alone (mechanical theory), in which case it is not clear why out of thousands of possibilities this blind force should have chosen just the one way of arriving at suitability. Or, in order to escape this astounding chance, we attribute to nature, on the analogy of our own consciously suitable actions, a suitable functioning. We are to-day still faced with these two alternatives, of which science has hitherto invariably chosen the second. The second alternative is better than the superficial notion that suitability arises in our own minds. For such a suggested origin is no small matter; since the whole external world exists in our ideas, our whole powers of knowledge might be all credibility, on the ground that it is mere appearance derived from our own minds, as indeed has actually happened (Petersen). But we must distinguish here between these fundamentals of our powers of knowledge, without which any representation of real, empirical objects and their changes is impossible, and those which render judgment possible concerning objects already scientifically known.

We shall see in a moment that we may decide between Kant's alternatives on grounds not yet considered, by asking whether nature really has employed thousands of different ways of bringing forth her creatures. Light will then be thrown on the question of suitability from quite a fresh side [para. 24].

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(II) General Morphology and Ætiology.

(A) The Basis of the Distinction.

Para. 20.—Having defined the fundamental conceptions of life we can now proceed to an investigation of those questions which are incident to every phenomenon of life : the laws of the formation of form and its differentiation (ætiology), and the principles according to which we evaluate form (morphology). Morphology certainly possesses for the anatomy of man great but not exclusive importance. The first step that we have to take is to show in how far the methodological classification into formal (architectonic) and ætiological (technical) considerations, upon which the whole of our conception is based, is logically correct. When we speak of our method of consideration it must be repeatedly affirmed that we are dealing with our attitude to things, not with any distinction inherent in the things themselves [para. 1]. We contemplate objects from two points of view according as we consider more their permanency or more their suitability.

If the objects were only in space, there would be three dimensions without change. If they were only in time, there would be only one dimensional change without body. Since they are, however, in time and space simultaneously, so we have a changing body-world whose objects show permanence and change simultaneously, and therefore conjointly present themselves to our minds.

The expressions, "real objects exist for us" and "stand in conjunction with one another," are therefore the same. The representation of this connection does not arise from experience, but each experience, even those which a child undergoes, presupposes the representation of objects related to one another. This a priori necessity of the appreciation of the relatedness of all our perceptions cannot be described by a name, since it differs in various ways according to the mode of representation. It may arise as a logical necessity, and then appears as a fundamental causal relationship. It can be a psychological necessity, and then acts as a driving force in behaviour. It can arise from the necessity of the sequence of changes in time, and is then interpreted as causality. It can finally apprehend the relationship of objects visible at the same moment, as, for example, the similarity of two objects. It can then be evaluated as the principle of proportion in the widest sense. Schopenhauer describes all these types of the a priori relationship as "the fundamental law." In all our ideas there is a relationship subject to laws and a priori definable as to form, but this does not make anything existing or independent, isolated or detached become an object for us [Basal law, para. 16].

It is now clear that for the representation of nature only two of these laws come into consideration. The one which underlies the inherent relationship of two events in time is the law of the sufficient reason of events (*Principium rationis sufficientis fiendi*) ; the other, which governs the relationship of the form of two structures, is the law of the sufficient reason of existence (*Principium rationis sufficientis essendi*). The first includes the law of causalty ; causation, though not always viewed in the sense here put forward, is at all events generally regarded as a fundamental law of the investigation of natural phenomena. The second law, which includes the methods of measurement and comparison, has hitherto only been recognized as a constitutional principle in geometry. It will, however, become clear that it has a far wider application in the region of form, though this has only been brought out here for the first time. We will speak in the following, first, of the principles of change and then of principles of permanence.

(1) The Principles of Change.

Para. 21.—This principle, though essentially only one, is yet met with in twofold form, of which one has been seen as the law of causation hitherto regarded as unique in organic nature, whilst the other, the statistical principle, has long since acquired validity in physics. Their significance for the changes which occur among organisms will be here placed in a correct light.

(i) Causal Principle.

If there were between death and life only a purely temporal relation, if we only knew that all men must die, then there would perhaps be a philosophy, but there would be no healing art, no dietetic, no macrobiotic. Only because we know that there is not only a temporal relationship between life and death, but rather a definite connection between the occurrence of death and another occurrence happening yet in life, which indeed occasioned the death, only in this way do we know a cause of death. Only the a priori truth that there is a cause of death makes it possible to investigate these causes, to avoid them, and to alleviate them.

Accordingly the old oft-refuted statement, which has recently been made again, is demolished by a single unexceptional example ; namely, the statement that all consequence is only a sequence in time. It is more. It is the lawful connection by change of two events following one another in time.

"Every effect begins as a change and is a reliable indication of some preceding change, which in relation to it is called cause [Basal law, para. 20, cf. scheme, first series]. The causal connection is concerned therefore only with change and, particularly considered, demonstrates the lawful connection of two changes, of which one transforms an existing condition and the other causes the development of a new condition (cf. Scheme 1). Since this change of state cannot be defined without objection it suffices to apply the law of causation to two states joined to one another by a change, and to describe as cause the whole state," producing what follows (scheme, series 2). The fundamental fact to realize here is that the laws of causation apply only to changes of material state and absolutely to nothing else. Consequently they should not be applied where there is no reason for them.

Scheme.

1)

$$\begin{array}{l} \text{State A} \\ | \\ \left.\begin{array}{l}\text{Change—cause}\\ | \\ \text{Change—effect}\end{array}\right\} \text{causal relation} \\ | \\ \text{State B}\end{array}$$

(2)

$$\begin{array}{l} \left.\begin{array}{c}\text{State A}\\ + \\ \text{Change}\end{array}\right\} \text{cause} \\ | \\ \left.\begin{array}{c}\text{Change}\\ + \\ \text{State B}\end{array}\right\} \text{effect}\end{array}$$

After this preliminary presentation of the laws of causation we pass to a more detailed consideration of them, and consider firstly the form they assume when applied to the organic world.

Just as it is easy for most, though not for all, relationships in the inorganic world to distinguish the two successive states from one another, so it is most difficult to distinguish them in the organic world. Quite often difficulties arise in the inorganic world. In an explosion it is not necessary that a flame should be carried into a space filled with gas. The flame can be in the space first and the gas stream in afterwards. The light and the gas can be present without danger if a window be open, and the critical moment arise through the closing of the window. The fall of an apple from a tree arises from a condition to whose formation contribute the effect of gravity, the condition of the stem, the warmth of the sun, and many other factors. A complicated example (Marbe) is the following, according to which an old man getting out of a train from a carriage which stops beyond the end of the platform on to frozen ground falls heavily and breaks his thigh. He dies in consequence of the fracture. What is the cause of the fatal event? The unusual position of the train? The ice? The distance from the ground? His age? The cause of inflammation of the lungs leads to similar difficulties, for under similar conditions only one of two men may suffer. Is it due to Fraenkel's diplococcus? The weather? The condition of the bronchial mucous membrane? The situation of the patient? Considerations such as these have induced us to recognize, in the sense of Schopenhauer, as cause (total cause), all the conditions preceding any state. In agreement with Schopenhauer's conception and supported by a more recent idea (Jensen) we name the more or less numerous components of the state, its system of determination; the determining factor which effectively changes the state Schopenhauer called the "Ursache Kat Exochen." We call it the complementary cause.

Also in the organic world it is necessary to avoid describing one individual thing as cause. Quite broadly, but quite rightly, Roux includes in causation all the internal and all the external factors which contribute to a certain state. The complementary cause according to him is the "releasing factor" which in many cases coincides with the so-called realization factor (or several of them). So under similar external conditions the fertilized egg is the cause, and the fertilization itself the complementary cause of the whole of development.

For the simplification of the combination it seems not only desirable but imperative for the analysis of normal processes to omit all those similar external conditions from the definition of causes and to regard that which behaves as the releasing factor as the "stimulus."

The whole complex of internal factors is then left as a cause which possesses a wider or a narrower range according to the circumstances under consideration. If we describe the stimulation of a nerve as the cause of a muscle contraction it is only in reality a complementary cause, while the whole arrangement in the system, central organ, nerve, muscle, skeleton, should be regarded as the cause in the stricter sense, and these again can only be artificially abstracted from a larger system of determinants.

If we inquire the cause of a certain organism, e.g., of the presence of human characteristics, we find only one possible answer, viz., that the cause lies in the condition of the fertilized human ovum (system-conditions, constitution). Leaving on one side the factor of fertilization, we are left with the significance of an actual germ plasm as the cause of the form developing from it. Since every such primordium is a specific one (of man, ape, dog, etc.), we may speak of a specific energy, not merely of the sense cells, but also of the sex cells and of other forms embodying a group of constitutions. The quality of the effect would thus be transferred to the condition of the causative system. The specificially reacting living system being thus placed between cause and effect, the cause-effect relation would be traceable, quite generally, to a quantitative factor, and would have to be subordinated to the law of the conservation of energy, as has been done first by Robert Mayer and later in a noteworthy article by Hueppe.

Before discussing this subject further, we must look more closely at the idea of cause and of system-conditions.

It is not easy to form a sure verdict, based on recent literature, on the subject of cause. We may adopt the above-given explanation, as the clearest, as the basis of our own. There are, however, objections to it (particularly those of Becher) which must be briefly mentioned. That a result is only a sequence in time, which becomes an idea of cause and effect as the result of habit and association, is the old view of Hume. This view reappears in recent times in the form that "no succession can easily be found, which is not simultaneously causal" (Becher). Even the famous example of day and night, which follow one another without standing in the relation of cause and effect, has been fitted in to the above assertion by making night follow, not day, but sunset. Even our example of death may be similarly interpreted by looking upon the cause of death as an event preceding death. The fallacy lies obviously in the fact that, once we have recognized it as such, we must subordinate every causal relation to another (the resultant) in time too. It is not merely the result which comes into question, but also, for instance, in the case of day and night, cause of death and death, the immediately preceding alteration of just this one condition, an alteration made by us. Only in so far as we are able to establish a chain of such alterations is succession in many cases at the same time causality. An example will show that this admits of no generalization. Let us suppose that we see several men leaving a building at intervals of five minutes. The conclusion we come to will differ according as this interval is due to equality of the length of time occupied by business in the building or to the fact that each man is directly called out of the building by the preceding one. Only in the latter case is the exit of the second man a result of the exit of the first; while in the former case the exits form a pure succession, which, of course, depends upon a more remote cause, viz., the length of time occupied in business. Like everything else, the man's exit from the building has a cause, but the exit of the first man is in this case not the immediately preceding alteration which leads to the exit of the second, and that is the whole point.

It has further been supposed by some that the relationship between cause and effect was no more than a particular case of that between reason and result, i.e., that causality should be interpreted logically only because it was a question of the combination of two judgments, e.g., the tree is burning because the lightning has struck (two judgments—the tree is burning, the lightning has struck). This view, too, avoiding as it does the contrast between the logical and the empirical reason, is undoubtedly false, for this view too goes back to an alteration of circumstances, and it is upon this that the causal relationship is based. Looked at from the standpoint of causality the tree is not burning because the lightning has struck it, but because the wood of the tree has been warmed to such a degree that ignition has occurred.

The objection that causality is not synonymous with real necessity also fails to meet the point. Causality in itself merely states something about one single change and its result. But this is invariably necessary, just as a definite change must of necessity have preceded every effect. The inventor of gunpowder certainly knew nothing about the necessity of ignition when a complementary cause was present. But that does not prove the ensuing change had no necessary result (see below).

It is especially necessary to beware of identifying the cause with an object, and of then speaking of the effect of one object upon another. Schopenhauer especially warns us against this. This "substantial causal idea" is entirely false. When a shot bursts the skull, we certainly speak of it as the effect of the shot. Scientifically, however, the cause is the change in intracranial pressure. The shot is the complementary cause acting upon the condition of intracranial pressure leading to bursting of the skull. This reflection must be applied *inter alia* to organic development. It is quite wrong to say that the tree is the cause of the fruit. The cause of the fruit is rather that change in the blooms which has led up to the formation of the fruit. Other changes lie behind, till we come to the change in the seed from which the tree grew. The whole process may be expressed as a series: Condition—change—condition, etc.; every phase of embryonal development is the result of the preceding one and the cause of the succeeding one, having regard to all the internal and external system conditions and the realizing factors. The immediate cause of the gastrula is the whole condition of the blastula, together with the changes taking place therein; the cause of the "neurula" formation is the completed gastrula in all its parts, together with the changes taking place, for instance, in the dorsal lip of the blastopore. With such processes as these, several separate chains of causes run side by side, so that we have apparently many changes taking place at one and the same time. In actual fact, however, even in these cases we have a simple succession (Marbe).

One further interpretation of causality must be mentioned, an interpretation which has much in its favour (recently, *Triepel*), and much against it. This is the interpretation of causality as a function in the mathematical sense. Its justification lies in the fact that causality is, in fact, concerned with the dependence of two conditions upon one another. But this kind of function cannot be regarded purely mathematically, for it exists without causal relationship (Becher), e.g., the mathematical functions themselves. In the applied sense the idea of function is often a useful symbol for the phenomenon of the connection, following certain laws, between various causes and various effects; thus we may say that rate of development=f (germ plasm+temperature). By this is meant, that the rate of development of two exactly similar (frog's) eggs will vary with varying temperature, increasing as the temperature rises, decreasing as it falls. But this does not exactly mirror the true causal relationship; for this consists in the fact that with two different primordia the same temperature produces a different effect, so that the temperature is not the cause of the rate of development, but only one among several stimuli. The substitution of a (mathematical) function for the idea of causality is, therefore, not recommended, because it may easily lead to the obscuring of the most important point, namely, the immediate relationship in which the starting point stands to that which follows. The modern misuse of the word "dependent" must be rejected above all; it originates in most cases from its convenience and is likely to hinder any penetrating search for cause. Death is not "dependent" upon disease, but follows it.

To call causality "subjection to law" is satisfactory for physical science (Häring), but not for changes in the organic world, where the great variety of changes of differing significance makes their description as "subjection to law" difficult. The fact that every normal fertilization is normally followed by development is certainly according to law. But the laws of gastrulation have not yet been discovered, because the complex of system conditions has not yet been unravelled, and we are still in the dark as to its real character.

Para. 22. To this critical study of causality little remains to add as to the origin of the law of causality. Causality certainly does not originate in our thought; it is no judgment of things, as Kant considered it. For, since all judgments are based ultimately upon material derived from perception [para. 5], but perpetual representations cannot be obtained without causality, then causality must be precedent to all thought, and all perception. Since for us the combination of objects originates in perception in time and space, causality is only another term for pure perception in time and space a priori; causality is the form of perception by which alone we have a real external world and in it the representation of change of objects. Thus we can only acquire experience, as we do from childhood on, and knowledge, upon a basis of the a priori category of causality which does not originate in experience. When we call an object "hard," we have learnt by trying. A priori, all that we can say is that between our act of touch and our sensation a combination is simultaneously conceived by us, by means of which we relate the sensation as result to the touch as cause.

All conceptions, judgments and conclusions as to causal relationship thus originate in perception and experience, and in particular is this true of conceptions of functioning and necessity. We may distinguish between an objective and a subjective necessity. The statement, everything which happens is necessary, means that everything which happens is the result of a preceding change in some system of conditions. And this is itself the effect of an earlier change, so that however far one looks back the causal chain is unbroken and without beginning. Looking forward, too, objective necessity exists in so far as no change is without effect. But no subjective necessity comes into the question, viz., an expectation, leading to the conclusion, not that a change must have an effect, but that the same cause will always have the same effect. Unlike a logical conclusion which is invariably a necessity of thought, this conclusion from one occurrence to another future occurrence is not necessary in thought, and is only more or less true, though often approaching so closely to truth that it may be regarded as certain.

That death occurs immediately after a man's decapitation is as good as certain, but this cannot be stated as an absolute law in view of the fact that birds can run about in a similar headless state; if reports may be believed, the same thing may happen with man in very rare exceptional cases.

We introduce into nature presumptively a submissiveness and a lawfulness (Becher), and on the basis of this we make rules (general) and laws (without exception) for nature. As to the origin of these premises of submission to rules and laws, it is not easy to say anything with certainty. To describe them simply as demands of the healthy human understanding (Becher) is inadequate; as we shall see, they are connected with the idea of the probable, and from this standpoint we can gain a better understanding of their origin [para. 24].

Para. 23. Let us turn to a discussion of the conditioning circumstances. In view of the unusual complication of the system-conditions and of the difficult philosophic considerations which are required for any exact account of the idea of cause, practical scientists have avoided concerning themselves with cause on the plea that natural science was concerned with the determination of the whole conditions of anything. This has been called conditionalism (Verworn, Hausemann), as opposed to causalism, by which is meant that a process is dependent upon such and such conditions. The colourlessness, even the lack of meaning of the word "dependent," has already been pointed out, and the same is true of the words "conditioned by" something. "Dependent from" or "conditioned by" something loses sight of the causal relationship which consists in change. The aim of causal investigation, viz., the determination of that state, as a whole, which, as immediate cause, brings about another state, can at most be attained by "conditional" investigation at one remove. There can be no question of replacing causal by conditional methods.

None the less there are important tasks for conditional methods of investigation. First of all, it is important to ascertain those conditions which are complementary causes; further, to attempt an analysis of all conditions which actually have any influence upon an occurrence. Both these tasks belong essentially to experimental embryology. In the terminology of experimental embryology [cf. paras. 85, 86], the partial causes of anything (e.g., gravity, light, temperature, moisture, oxygen, etc.) are termed "factors," which are not regarded, like algebraic factors, as connected with the multiplication sign, but as positive and negative forces strengthening and weakening one another. Each factor can itself be made up of partial factors, called "components" (e.g., the altered concentration of salt-content of a fluid as factor in the development of an egg can consist of components which partly increase the rate of development, partly alter the osmotic relations, etc.). Invariable factors, which remain constant for a given development of a given egg (e.g., specific gravity, permeability of the cell membranes) are "coefficients" of development. The sum of all the factors can be grouped from a variety of standpoints: (simple and compound; the latter, mostly in the organic world, also called complex factors; factors of solution and of stimulus, time factors). For our purpose the important grouping is that which divides them into factors of determination and realization [paras. 85, 86].

It is a pity that this investigation is called "causal," though the term is now so ingrained that there must be difficulty in getting rid of it. We speak, for example, of the "cause" of the beginning of bone structure, of the cause of the form of the heart, etc. Every development of a single organ is, however, only a "partial occurrence" which obtains significance only with regard to the whole occurrence. We can neither completely comprehend the form of the parts of an organism without reference to the whole, nor understand the partial cause without connecting it with the whole cause. For it is the development of the whole which first supplies the system-conditions for the development of the individual part. And so we may distinguish between the aims of causal and conditional investigation, by referring to the former the question of the origin of the whole organism, i.e., its system-conditions, while the latter has to deal with the nature and activity of the system-conditions themselves. The causal is thus the more comprehensive and is concerned with the reasons for the formation of organisms (phylogenesis); the latter is more limited in its scope, which deals with the manner of the origin of the individual organism (ontogenesis). The "why" of ontogenesis would be answered if we knew how a typical cell was produced. Adopting Rauber's terminology we may describe the two developmental series as protogenesis (origin of the first hen's egg) and deuterogenesis (a chicken is now invariably produced from every hen's egg).

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(ii) **Statistical Obedience to Law.**

Para. 24. In view of the enormous number of causes contributory to any occurrence the possibility of the renewal of identical combinations and therefore of identical events is definitely excluded. If, in spite of this, certain occurrences, forms, or processes are commoner than others, if we even go so far as not merely to expect certain changes but to rely upon them as certain, then we must have some justification for this. No justification is to be found in any assumption of obedience to laws thrust upon the world by our "healthy human understanding" (Becher). "Similarity in the world" (Marbe) is indicated with greater certainty by statistical science, so that the presumption of obedience to law is in itself nothing but a reliance upon statistics. The science of statistics asserts that of all possibilities only a very small number are actually realized, and that the realized cases group themselves about an average situated roughly equidistant from the mathematically possible limits. The theory of probabilities says much the same. With this distinction, however, that it deals with all possibilities, while statistics take into account only those actually realized (cf. Thaer). The essence of statistics is to show that the mathematically less probable and impossible cases actually occur seldom or not at all (Marbe).

The natural scientist may take up a third position with regard to all this ; he is as little satisfied with the "expectation" of a probability, a "presumption of obedience to law," without the ability to give a reason for this expectation, as with the determination of a phenomenon whose cause he cannot discover. His task is therefore the determination of objectively scientific probability.

We generally assign to the sphere of probability all those cases the causes and conditions of which are so numerous that we cannot be acquainted with them all. Their objective probability is, however, satisfied by our possession of a certain degree of knowledge of them upon which conclusions can be based, even though we have no complete knowledge of the sum total of the conditions (v. Kries, Smoluchowsky). Objective probability thus proceeds not from what is not known, but from what we do know. However complicated the complex of condition may be, we know the fact that within the wide range which all systems of condition possess in regard to their presence or absence or with regard to grouping, certain group-systems have greater or less probability; with repeated throws of the dice, the form of the dicebox and the shaking movement become nearly constant, in any case unusual movements of the hand become more rare, and accordingly the dice may be expected to fall on an average very similarly (cf. Marbe, Bd. II, Chap. 7, "On games of skill and work," if by a chance correct throw at the beginning a prize has been obtained, then other prizes follow easily). The conditions under which red will turn up ten times running in roulette are very small in relation to the whole range of possibilities. On this knowledge of the total possibilities our assumption of objective probabilities and improbabilities is based (v. Kries).

With regard to variable factors, too, it is possible to trace the origin of a probability to objective features (e.g., in the game of cup and ball, movements of the joints which chance to be correctly judged lead to a stopping of the arm movement). This "chance" is objective (von Kries) or regulated (Smoluchowsky) chance. It thus acquires the significance of a regulated factor intruding upon the causal series, the factor of a calculable possibility. If this objective chance be analysed its essence will be found to exist in the fact that small causes produce great varieties and that the characteristic factor possesses the nature of an oscillating primary occurrence with approximately like prospects of the occurrence of all phases of this oscillation. A dice falling upon its corner may be taken as an example (Smoluchowsky). The slightest inclination towards one side necessarily causes it to fall upon a certain surface, an event which always depends upon the position of the centre of gravity and its distance from the surface of the table. Regulated chance is thus a variable cause, the occurrence of which is determined by a regular distribution factor (Smoluchowsky). The distribution forms here one possibility; since this, being equally great, is calculable, so also is the appearance of any number when throwing one die equally great.

Since it is impossible to prove all the possibilities of distribution, one is obliged to take a single one in a *single* case and to verify it by repetition in a number of cases. It is on this, according to this view, that the significance of large numbers in statistics rests, and not on the fact that it is from them that we first recognize a probability (von Kries). If we proceed from possibilities which lead to certain results and whose frequency can be calculated, we have to deal with an objective probability entirely independent of man.

It is just because of the unusual complexity of all conditions on the one hand and of the uniformity of so many processes and formations that in "objective probability" the possibility exists for natural science of regarding much as subject to laws which cannot be regarded as subject to the laws of causality in the strict sense of the words. Above all, it is in this and not in any "presumption of obedience to law" (Becher) that the basis from which laws may be deduced from continually recurring individual observations is to be found. For we may rightly conclude that within the total area of variation of all possible conditions those which, after thousands of repetitions of an occurrence, have never co-existed, will never co-exist in the future either. Therefore if we are right in saying that a presumption of necessity (e.g., that death follows decapitation [para. 22]) is not possible with the same degree of certainty on grounds of causality as the logical necessity (e.g., of a conclusion) is (Becher), then it follows that all obedience to law is ultimately no more than a statistical obedience. The distinction between law (that which always happens) and rule (that which generally happens) (Roux) would gain in clearness if based upon statistics. This becomes particularly significant in cases in which we cannot refer to "causes," but have to be content with the assertion "that things are in fact so and so" (von Kries); in other words, in that state which mathematicians term "the primary conditions . . . which are not established by a universal definition, but are only to be regarded as something actually existing." We are exactly in this position with regard to the organic world, the primary conditions of which we do not know, but have to assume as something actually existing. These primary conditions are the germ-plasm of the species cells.

Reliance upon the similarity of the range of variation, i.e., upon the similarity of conditions, then becomes the explanatory principle of the similarity of phenomena. The fact that similarity plays a dominant part in natural science, and above all in scientific anatomy, shows to what extent the introduction of statistical obedience to law in this branch of science is justified. Apart from the fact that we have to assume "cosmic primary conditions," the earliest forms of life, and primary conditions in general, the species cells, without any possibility whatever of establishing their causal descent, the similarity of the organic world is shown in three important phenomena:—

(1) In the similarity of genera to one another.
(2) In the similarity of descendants.
(3) In the similarity of the individuals of a species.

The bond which unites similar forms can be termed, quite generally, inheritance—a name for a fact and a process as to the nature of which we are completely in the dark, but which, at any rate, serves to maintain similarity. Even those changes of the germ plasm, now called mutation, which have increased the number of forms by the production of new ones, have not produced phylogenetic monsters, but creatures in which it is always possible to recognize the similarity which persists between them and others.

Let us now regard all these similarities as the result of highly probable combination processes, which we may attribute to similar kinds of variation of the material developmental potentialities. It is quite certain that this is the case with similarity within the forms of one species, i.e., in the formation of the individual. The Mendelian rules in their strict form are the visible expression of this effect of the same range of variation. Where they do not appear in strict form, the existence of initial limits of variation may safely be concluded, disturbing the uniformity of the distribution of the oscillating factor, as has already been proved empirically by V. Häcker. Amphimixis (crossing) points to uniformity within the larger groups of the animal kingdom, a probability which is increased by other considerations [para. 109]. Has not amphimixis, ever since it has been known, been looked upon as Nature's principal method of maintaining uniformity side by side with new combinations? The greatest difficulty arises in the case of the phylogenetic origin of something new (mutations). It is true that monsters, such as for instance Empedocles, supposed to originate in the blind minglings of the elements, are not found; but hints of such "improbable" forms exist. They are termed "failures" in adaptation (Abel), e.g., animals with a useless number of carpal bones, many excessive or giant formations leading to the extinction of those possessing them (developmental offshoots), fishes with gigantic upper jaws which have to break off before they can be of use, animals with tusks which pierce the upper lip, and so on. It is very remarkable that, if we look at animal forms as a whole, we find a greater number of forms at the beginning of each class than we do later, and that from this initial abundance only a few are continued into later epochs. The remnants of the primitive fishes point to a multiplicity of forms of which recent fishes show only scanty traces. The gigantic forms of the Jurassic stegocephals are represented to-day by the few known forms of amphibians and reptiles. Creation has thus become not only more similar, but also more uniform.

If we could regard the structure of the germ plasm as being simply molecular, we could use the statistical obedience to law to explain the similarity of forms in the same way as it is now used (Boltzmann, Planck, cf. Loria) to explain the Brownian molecular movement or the law of similar positions of the molecules of a gas. (If all possible movements of the molecules actually took place, there would be no oscillating Brownian molecular movement; rather is it the case that the initial disorder is converted into order by the mutual influences of the moving molecules.) With regard to the Brownian molecular movement this assumption is proved experimentally by the fact that, even with completely orderly movement of the whole system, disorderly zig-zag movements of the single molecule can be made visible with the ultra-microscope (Ehrenhaft). This state of order is, compared with the initial state of lack of order, the more probable. Above all, it is significant that the irreversible process of the conversion of energy into warmth is, according to this principle, no more than a transition from improbable to probable conditions, and that in this case the more probable state contains the indication of later time (Planck), while with reversible processes the indication of time plays no part. The terms "probable" and "improbable" have justly been objected to here (von Kries), because every realized process is in itself probable, and we ought to speak of states of greater or of less order. We are, however, right in stating that the so-called more probable state is so because disturbances of the equilibrium, which has once been attained, are no longer to be anticipated.

What a wonderful fact it is that the law of non-reversibility of phylogenetic development (Dollo's law, cf. Abel) has been determined empirically long ago. It is beyond all doubt that an element of non-reversibility, in the sense of an advancing, no longer disturbable, order, exists in the formative processes (cf. Häcker 22, Just 22, Kranichfeld 22, Nopcsa 23, Lubosch 24, 25). Characteristics which have become definitely inheritable are universally accepted as non-reversible, particularly those which are of "complex cause" (Hacker.)

Apparent reversibility certainly occurs, but it is to be noted that in cases where creatures of a higher order appear to revert to characteristics of a more primitive type, the genealogical connections should first be explained. The possibility that the apparently reversed characteristics have not been inherited on special lines cannot be excluded. Such examples are, however, so rare that they have to be sought (Nopesa). The non-inheritable characteristics naturally disappear; for these may be reversible as soon as the external stimulations revert to their original form. Thus the well-known Steinheim snails (Planorbis) revert at the highest stages to the original form, presumably because the changes which are present in the intermediate stages had arisen as the result of hot springs.

Is organic irreversibility, however, more than a mere similitude? One thing at any rate is probable, viz., that mutation arose in the shape of a "disturbance," that this disturbance was overcome, and that conditions quickly introduce similarity, a state of order. It is also certain that Nature makes use of means known to us in order to limit the complexities of system-conditions (limits of variation). We have in mind the coupling of factors [para. 109], homozygous gametes hindering division, the formation of "collective chromosomes," the reduction of the number of chromosomes within phylogenetically younger species [para. 116]. All these can be regarded as examples of such means which restrict the area of variation of the conditions. Further questions naturally arise, e.g., the question in what relation increase of similarity stands to the development of inner differentiation [para. 84], and above all, the question of the molecular structure of organic life, which can certainly not be sufficiently explained by reference to the molecular theory of gases. If this is to be regarded as a dispersion (in a gaseous medium), if Brownian movement is a movement in a colloid solution, if colloidal metal solutions show a phenomenon resembling that movement, yet the structure of the living protoplasm is distinguished from even highly complex colloids by numerous features of a structural nature of which we are still ignorant (chromosomes). Here, therefore, we are completely in the dark, although the key to the understanding of the development of forms must undoubtedly lie hidden in these complications.

Obedience to law in the inorganic world may be taken as a fact now universally accepted. With regard to its significance for the development of living forms, it must still be termed a hypothesis. Briefly stated, this hypothesis might run as follows: The development of organisms has been and is governed by "regulated" chance, the result of which is the maintenance of and constant decrease in multiplicity of forms.

In this discussion we have not made any detailed examination of all the theoretical problems of the theory of probability and chance (cf. Smoluchowsky, von Kries, Marbe, Thaer; the latter's remarks on probability and species-formation show little divergence from our own view). This may, perhaps, be the more readily forgiven because we have attempted to show that no fundamental contradictions exist between causality and the expectation of probability, and therefore between probability and obedience to statistical law, as is clearly seen from the definition of objective regulated chance. The inviolability of the law of causality remains untouched.

Since the law of causality is to be regarded as inviolable in the hypothesis of regulated chance in the development of form, it follows that we get an insight of a quite especial kind into the problem of suitability to purpose. This hypothesis answers in the negative that question with which we closed paragraph 19, the question whether nature really has, as Kant supposed, thousands of ways of producing her organisms. So long as we imagine that blind chance reigns, Nature is for us like that gigantic library filling the whole cosmos (Katheriner of Braus), which owes its origin to combinations of the letters of the alphabet and must comprise every work of poesy, present and to come, without the possibility of our finding a single one of the books, because the library fills the the whole cosmos. We are obliged, then, to look to teleology in some shape or form for help. Actually, however, to stick to the metaphor, those books and those alone are produced in Nature. If the hypothesis of regulated chance is correct, there was no blind mechanical force, and there were no thousands of ways, but only a few; and all those ways which were followed were the only possible ones. But then according to the logical laws of the hypothetical conclusion, the reason for assuming finality disappears in Kant's alternatives. For that which came about as the only possibility was capable of life, capable of maintaining and adapting itself, was the beginning of suitability to purpose; so that in organisms there can be only that which is necessary for form [cf. dysteleological features, para. 19] and adapted to function. Science, in talking hitherto of suitable development, in the sense of a development directed towards an aim, was merely transforming regulated chance, which stands at the beginning of the paths of development, into the will of the individual organisms, which had originated upon these paths. It would be like assuming that a man, desiring to throw the combination 3, 4, 5, fifty times in 100 throws with three dice, could attain his object by the ability to establish the limits of varation for this result.

Petersen derives suitability to purpose in similar fashion, by showing, by experiment, that a suitable organism renders the maximum of any given performance possible. A maximum can only be something unambiguous, obedient to law; thus that which is suitable to purpose is at the same time that which is actual, because it alone is obedient to law. This derivation, however, lacks firm ground, because we do not know how Nature proceeds with the creation of maxima and minima; she does not proceed by experiment. And she does not do it in every case, since our organs are not all optima, but only an approximation thereto. The solution can only be found on the basis of our own derivation.

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(2) Suitability to Purpose in Persistence.

Para. 25. Whoever examines all phenomena which can be brought within the compass of causal investigation must become aware that a large part of the world of Nature does not belong thereto, or at all events does not belong immediately. This large part comprises the whole world of forms, which we see quite generally as dot-like, linear, superficial and bodily forms. All these forms (Häring) are characterized by "determinations" of shape and size, as well as of position and direction in space, and further by the relations of these determinations to one another (relations of shape, size, position, direction, geometrical relations); by these relations alone is that "union" [para. 20] of objective representations effected, since the forms are unchangeable in time, and it is their union in space which alone concerns us. With regard to shape, which we see as a filling of space within definite limits, the relation is expressed by a judgment as to likeness, unlikeness, etc. The determination of size is concerned with "larger," "equal in size," "smaller"; the union of position-determination is expressed in the relations: interval, between, within, without, through, above, below, behind, in front of, left, right, in the middle. Relations of direction lead to a judgment of opposition and symmetry (Häring). It is clear at once that all these judgments rest, not on the recognition of causes, but upon observation alone. It is senseless to inquire why one line is longer than another, or why all the faces of a die are alike. Kant declared that a left glove can only be recognized as such by its appearance, and that it is impossible to explain *why* it is a left glove. This application of the law of sufficient reason of being is best shown by geometric and stereometric forms. We can see, but we cannot derive from a cause the fact that all the angles of a triangle together make two right angles, or that two parallel lines never meet. Geometrical (Euclidian) proofs of such facts are based upon spatial comparisons and upon the demonstration of the impossibility of the opposite (Schopenhauer).

Spatial comparison is the means for the determination of all purely spatial relations between forms; measurement is the most important method employed in this comparison, because we have always to deal with an indirect superposition or imposition. The system of co-ordinates makes it possible to fix objectively position and direction and to express them numerically.

It is quite plain that this principle of form applies not only to geometry, for which it was first set up, but also to a large field of forms, in the case of which questions as to cause are equally senseless.

Such are, first and foremost, architectural forms, and in general all such as can be expressed by number and measurement (and by rhythm), e.g., musical works. A Corinthian or Doric column can only be comprehended by observation; its parts can only be related to one another by measurement. Ornament, the shape of an eave, the order of a column admit of no question as to cause (apart from the fact that they have their cause in the artist's will). The form of a whole building, e.g., of a Gothic cathedral, admits of this question, in so far as the results of gravity are concerned. But once the constructive principle of directing the weight on to buttresses and flying buttresses is given, it is not possible to inquire why a pointed arch is more pointed in one cathedral and less so in another, or why walls carrying no load are pierced with wider openings in one case than in another. It is true that we can say that in view of the force of gravity a certain construction and a certain material have been selected, but we can give no reason why, when once the proportions of surface, weight, vaulting, etc., have been chosen, all the parts must stand in an inviolable spatial relation to one another.

The case is very similar with organic bodies. With them, too, we have shape, size, position and direction of the parts. As soon as we disregard the origin of form, i.e., as soon as we accept a form as given —which we are obliged to do since all extant forms are constant— it becomes clear that all inquiry as to cause is objectless here too. The shape appears in the first instance as an outline, superficially. As to the locus of all the points limiting the shape, this can with simple forms be calculated (conical, etc.), but cannot be determined causally (analytical measurement).

In certain cases such measurements have been made, e.g., in the analysis of articulations. But even when a joint form has been mathematically analysed to the utmost possible point, we have only succeeded in answering the question "how?" and not "why?" An analysis of the organs—not to mention the whole body—by means of a specific formula of structure, such as is theoretically possible (Häring), may perhaps be a possibility of the distant future.

From a comparison of shapes we arrive at a determination of their likeness, similarity or difference, features to which methods of causation cannot be applied.

Size is of great importance for organic forms. We know to-day that for the development of the form of organs and tissue, for the proportions of the body, even for many processes within the body [ossification, para. 41] and for the histological structure of the organs, size is of paramount significance. Even if we derive size of body from the size of the egg-cell and from the size of the body-cells, which is specific and typical for every species, the latter is no more a subject for causative investigation than is the question why the cubical contents of a die amount to 8 c.mm. The size of a cartilaginous element of the skeleton, for example, and indeed of any organ, depends necessarily upon the way in which the vessels are distributed within it (Spalteholz), and the inner structure of bone or of cartilage is dependent to a definite, demonstrable degree (v. Eggeling) upon the size of the whole body or the size of the skeleton. The material used also depends upon the total size of the body. We cannot imagine large and small elements of the skeleton as built of the same material, any more than such a thing is possible in manufactured objects. This has, for example, been proved for the material of which the sternal ribs are composed in mammals (Richter). And in the case of the position and direction of the parts of an organism we meet with the same state of things as is found in simple geometric bodies. If we apply a system of co-ordinates to the body and specify top, bottom, front, back, right, left, etc., it remains quite impossible for us to say why the back is the back and the front the front, why left is not right and vice versa. No causative determination of these features, no definition of the left, of thicknesss, depth, etc., is possible (Häring). Ideas of polarity (cranio-caudal direction) and of symmetry (direction from the axis towards the right or left) are of special significance. The proportions of the body are derived above all from determinations of position and direction and their relations to size. These proportions, which with certain limits of error even enable us to reconstruct the whole body from a given measurement, or a skeleton from a thigh bone, are present not only on a large scale; a similar proportion exists within the cells (nuclear plasma relation), and is of significance for the amount of growth and division of the cells and thus for the size of the body. These proportions are termed the canons of form and the nuclear plasma relation is a canon of this sort (Heidenhain); the consequent dynamic relationship between all the component parts of a cell is strictly regulated thereby (tonus, syntony). In the structures there occur in addition definite numerical relationships, beginning with the numbers of chromosomes and extending to the external formal features of the body. The number of the cells, which make up the animal or its organs, is in many cases normalized and constant [paras. 105, 106]. The number of vertebræ, ribs, scales, teeth, are instances. The fact that animals have two eyes and four extremities, and that fingers and toes do not exceed five in number, may possibly be capable of explanation in some way or other on the ground of suitability to purpose, but can never be explained causally. All these examples show that to a large extent organisms possess features which lie entirely outside the sphere of causal investigation. They form the subject of morphological examination, which deals with the persistent element amid the changes of form and with its determination from the point of view of its agreement and similarity with or its difference from others. The method employed is comparison, which is measurement in the widest sense. Comparison is not limited by size; it embraces forms in their entirety, the forms of parts, and the forms of the grosser, finer and finest elements, and may with complete justification be placed side by side with causality.

That part of morphology which deals with the stereometric aspect of organisms has long been separated under the name of promorphology (E. Haeckel). This separation is important because it indicates a contrast between organic and geometric form, which, in view of what has been said above, we cannot pass over. The morphology of organisms should be termed "causeless" only in so far as the phylogenetic (historical) development of forms is disregarded; there is further, as has already been pointed out [para. 9], an intermediate region between morphology and ætiology, the region which comprises consideration of the conditions for realization of form-development. Promorphology is, so far as one can see, much freer from the influence of these causes and conditions than morphology in the narrower sense. But even promorphology is not quite free, particularly from analysis of system-conditions, for the filling of space rests ultimately upon something of dynamic nature. A living form is not purely geometrical, for the total content of the elements of form in space, their position and direction, polarity and symmetry, is something active and must be based upon effects of the elements on one another. And finally, it is to be noted that, since living forms are subject to the processes of growth and decay, the question of "cause" arises in a different shape as soon as there are forms such as we actually meet with in the animal kingdom, and begin to ask how these forms have come about.

It is, therefore, not enough to differentiate the morphological and ætiological points of view and to define their functions; we shall have also to indicate what is common to both, and this forms the basis of our further examination.

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(B) Morphological and Ætiological Considerations of Organizations.

Para. 26. We now propose to consider what methods are employed by the morphologist and ætiologist, what results are reached and within what limits each manner of approaching the subject is possible. We shall first consider the :—

(1) Morphological Considerations.

Under this head we have to deal with two problems. Firstly, we must have a clear comprehension of the meaning of the concept of an organic form, and secondly, we have to examine form comparison.

(A) Form and Forms.

By the form of an object we mean its appearance in space, based upon the inner connection of its parts and independent of environment.

In organic nature such a form is possessed only by solid and in part by colloid bodies (fluid crystals), while fluid and gaseous bodies have no form peculiar to themselves but assume the form of their surroundings. Under certain conditions fluids assume the form of a drop as the result of surface forces. In the organic world many unicellular organisms apparently lack a definite form because their form is subject to continual change (amœbæ). Yet in every minutest interval of time a form is undoubtedly present [Malakomorphosis, Roux, para. 14] and the life of amœbæ is bound up with constant transition from one form to another. With multicellular organisms the surface is defined by the outline; this we call "form" in contrast to "structure" (inner form, Roux). The form or outline differs from the surface of inorganic bodies not fundamentally but only by its stereometrically incomprehensible peculiarity. We have already noted that form in organisms, as well as in the organic world, is not, as it is in geometrical figures, a mere outline, but is at the same time the expression of a dynamic equilibrium of numerous factors. It would not be quite correct to speak simply of a "force" holding the cells together. For we have already seen [para. 14] that a multicellular body is not composed of a number of parts; one cell of a metazoan body is not formally equivalent to a unicellular organism, but always the whole body. It is only the fertilized egg-cell which in regard to form repeats the unicellular stage.

In spite of the fundamental similarity between forms in nature, one important point of difference must not be overlooked. This is the fact that, apart from the change of form of amœbæ, forms are to a high degree variable in time, with the result that an organism passes through various states of form during its life. So great is the difference in form between the fertilized egg-cell, the embryo at various months, the new-born infant, the youth, the adult and the aged, that they might be taken for different beings, as has actually happened with the larval stages of certain creatures whose metamorphoses were not recognized. In spite of this we speak of the human "form," without regard to the differences of this form as seen both in individuals and in races. This proves that "form" in the organic world must be something more than the aspect of a single given surface. The subjective (psychological) factor, which enters into every idea of form, can never be got rid of in so far as we subordinate to it the forms of form-change. It is as if we dispensed with the immediate perception of the changes, i.e., the causal judgment, and could perceive the multiplicity of forms as an object in space. This power of perception, peculiar to man, is at the base of Schopenhauer's perception of ideas. These, as has already been said, are not ideas in the old sense of Plato, i.e., not creative primary pictures, but actual, if not real, objects; actual, because they are perceptible; unreal, because they lack the definition of relation in time to other objects (Schopenhauer).

Let the philosophical explanation of ideas be what it will, let philosophy deny altogether any justification for the assumption of their existence if it pleases, Nature teaches us of their existence beyond a doubt. Let us imagine that we have received some individual stages of development of the hypothetical beings from some strange planet, without being in the position to follow the developmental series to the end and not able to identify the organism, we should regard these stages, since they did not function, as having no relationship to the external world; they would appear entirely purposeless, as incomprehensible, irrational natural objects, supposing we could realize that they were natural objects at all. On the other hand, for one who has a knowledge of developmental history every separate stage of development is revealed in the final form; in the adult man we can see the embryonic forms, the embryonic cranial convolutions, the visceral arches and so on. This psychic process, without which we cannot speak of a form in view of individual forms, is no intellectual abstraction excluding the non-essential and holding fast the essential, for in that way the individual form would not be comprehensible. An intellectual abstraction certainly leads to more general representations of form, but the process of which we are speaking now is different; it may best be described as the maintenance of memory pictures side by side, which unite to form a unique whole, a new creation of our own.

We make the same new creation not only when looking at a single form-stage of a final form, but also when we contemplate a number of individual forms which we unite to form a conception of a complex organization, e.g., when we imagine a composite picture of mankind which combines the features of all the races of man. A special feature of such a new creation is the fact that, while it is only realizable in isolated cases, yet in no isolated case does it possess that actuality with which it becomes alive to us as a composite picture. This composite picture we have hitherto called the "idea"; from now on we shall give it the classical term, "type." By this means we arrive at the differentiation of form and individual form, the distinction between the type of form and its individual cases. This involves our recognition of the fact that in all study of form we do not proceed purely intuitively in the lower sense, but that unconsciously our attitude to Nature is one of a more comprehensive perception, which is entirely different from an intellectual abstraction. We shall see that the actual appearance of the type (= union of all conceivable cases) can be deduced from the standpoint of the combination of the most probable, and possibly can only be understood in that way. Perception of type and abstraction of the concept of form are, as we shall quickly see, the two important foundations of subjective comparison of form.

Para. 27.—Before turning to this point, we must examine the inner division of organisms as opposed to their external form. If the latter falls under the heads of shape and size [para. 25], the former comes within the sphere of position and direction. From the determination of these points and their relationship proceed conditions the value of which for morphology cannot be over-estimated and which give us the law of topographical constancy.

The relative positions of muscles and bones, of the bones to one another, of the vessels and nerves to one another and to the muscles and bones, is so definitely fixed that all possibility of a surgical operation or clinical diagnosis depends solely upon them. The determination of interference with sensibility in a small region of the skin makes it possible for us to predict with certainty in every man and animal the occurrence of a disturbance at a definite spot in the spinal cord or brain. One of the objects of our teaching is the learning of this constant position of the organs.

The topography of the organs rests on two rules, so inviolable as to possess the value of laws, whether we view them from the causal or the statistical standpoint. The first of these laws declares that the connections of an organ with its surroundings are constant and recurrent. Thus, in every animal in which it exists at all, the upper jaw stands in the same relation to the premaxilla, the zygoma, the frontal bone, etc. The lungs are always situated ventrally to the foregut, the aorta with its arterial arches always embraces the pharynx. The trunk of the vagus always lies behind the internal carotid with the same constancy as the small artery to the sternomastoid passes in front of the hypoglossal nerve. The second law states that an individual part may differ in size in different animals, and even be entirely wanting, but whenever it is present it never fails to have the typical relation. The coracoid uniting the scapula and the sternum can almost entirely disappear in the higher mammals and become a quite small process of the scapula (*processus coracoideus*). It is then no longer united with the sternum of course, but its situation beside the articular surface of the scapula persists under all circumstances. These two laws, recognized a hundred years ago by Geoffroy St. Hilaire as a "law of connections," lead to the idea of homology (Owen, 1848). Organs in like topographical relation are homologous. The inviolability of this law is shown by the fact that we can seek and find a wanted organ as we can a wanted planet. But in this case too individual variations exist and to a consideration of these we shall return in a later paragraph.

Another law of like significance is Geoffory St. Hilaire's "law of balance," expressed in poetic form by Goethe in his "Metamorphosis of Animals." This law declares that in degree of development the individual organ is dependent upon that of other organs; in fact, all proportions and, incidentally, the stability of the body rest on the inability of any one organ to disturb by its preponderance the harmony of the whole. A familiar illustration of this law is provided by the relation of the length of the neck in quadrupeds to the length of the fore-legs, which allows each animal to reach the ground with its lips. It is worth noting that a number of organs (cervical vertebræ, larynx, pharynx, muscles, vessels, nerves) have to undergo alteration to make this possible. We may imagine the same sort of thing in connection with a change in the teeth involving changes in the jaws, the skull and the muscles; an ape's head on a human vertebral column, or the reverse, is quite unthinkable. Limitation of the number of feet to two in the fossil gigantic reptiles, in birds, in marsupials, in apes and men, is always accompanied by characteristic features of the organization of the lower extremity (Weidenreich), of the proportions of the vertebral column, ribs, upper extremities and head, as well as of the position of the bones (pelvis, Nauck). The different kinds of two-footed animals differ from one another, but the general law applies to them all. We can see ex posteriori why this must be so, by experimenting in order to ascertain to what degree a part can be extended in order to give the maximum of usefulness, having regard to its weight, and the cross section of the active musculature.

Of course, no such experiment is made by Nature. A nearer illustration of the process is given by the purely geometric one of "correlative transformation," which transforms the same form by drawing it in a movable grid (see fig., 3*a* and 3*b*).

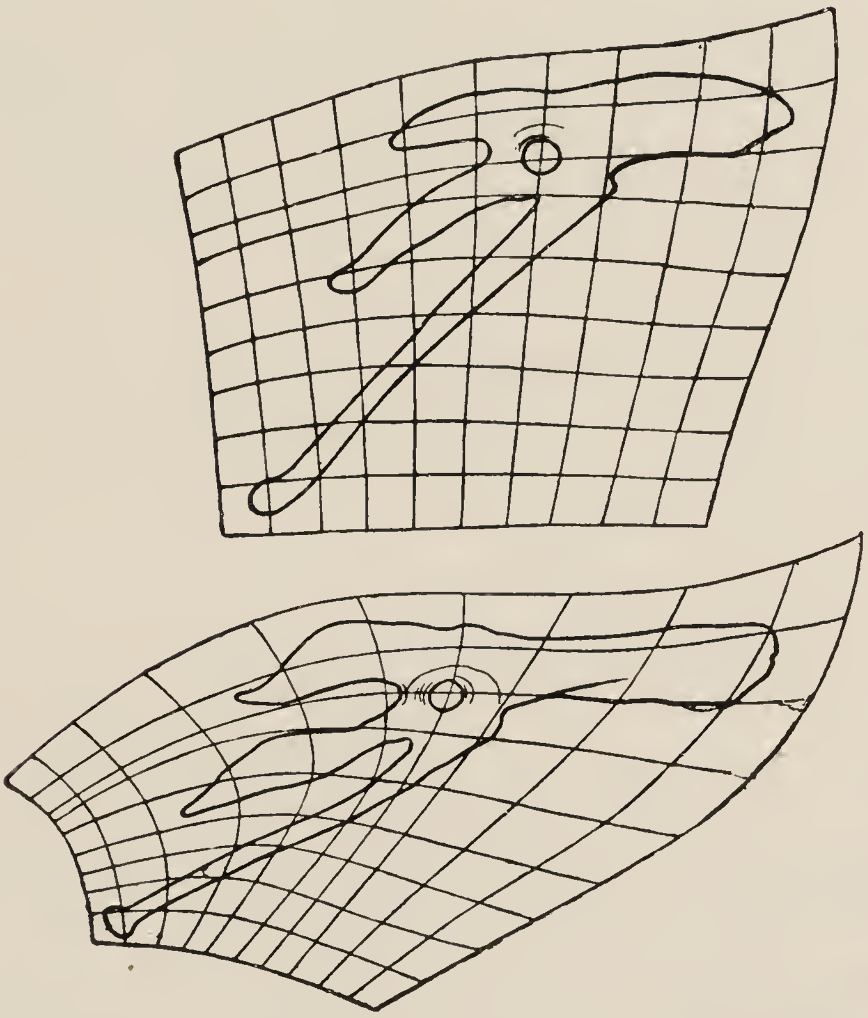

Fig. 3a and 3b.—Transformation of the pelvis of archæopteryx into that of apatornis by displacement of the grid. Explanation in the text. The pictures here reproduced (figs. 52 and 53 from Thompson, l.c.) are the first and third intermediate stages. The latter resembles almost perfectly the pelvis of apatornis.

The illustration shows the pelvis of apatornis and archæopteryx; the pelvis of the latter drawn within a square grid. The homologous points of the pelvis of archæopteryx were joined, giving a strangely distorted grid. By certain movements of the square grid it was possible to transform the archæopteryx pelvis into that of apatornis, using two intermediate forms. The surprising feature of this is the fact that the strange form of the apatornis pelvis with the ileum, ischium and pubis brought close together and increased in length (to the left in fig. 3b) and the continuation of the ileum are not due to functional influences but rest on increase or decrease of the width of the meshes of the grid. There is, however, no need of surprise if we understand the meaning of the grid as applied to an organization. A longer bone implies within a three-dimensional system of co-ordinates different "points" of the whole surface, which would necessarily involve disturbance and confusion of the entire system unless they were subjected to a general levelling out. Any such confusion must, however, be levelled out in the germ-plasm according to our hypothesis of "regulated chance," so that we have to trace the law of equilibrium (balance) not to subsequent experiment, but to the growth of a primarily probable combination [para. 24]. In this connection a remarkable fact is to be noted. Bolk gives a primitive picture of the shoulder and pelvic girdle as it would appear if the myotomes were attached thereto in serial order. This imaginary primitive picture reminds us strongly of primitive forms of the pelvic and shoulder girdle. The displacement of the myotomes and their union to form muscles would, according to this, present a part of the factors under the influence of which the grid-like changes in the shape of the skeleton have taken place.

But equilibrium is seen not only in the proportions (quantitative), but also in its qualitative aspect. Nature is able, for instance, to achieve the same end by means of calcification as by ossification. Is it mere chance that cartilaginous fishes possess not only calcified skeletal elements, but an abundantly ossified skin, or that toothless tortoises have a strong shell exactly as though a certain amount of bone had been allotted to the creature? We find quite generally that animals with poor sense of sight have a strong olfactory sense and vice versa; when we reflect that with the latter the skin is richly provided with glands and is hairy, while that of the former has but few glands and is covered with feathers, we see that we are faced with deep problems of combination which cannot be satisfied by a purely mechanical solution. Goethe was referring to such points as these in his poem already alluded to, when he said that no animal with horns has teeth in the upper jaw, and that Nature was quite unable "to create a lion with horns."

These laws of combination and equilibrium are true form-laws, and while they can only be verified ex-*post* by conditional examination of the system of determinants, they can only be determined ex-*ante* by pure contemplation, and can only be rendered comprehensible on the basis of statistical law. It is only an application of statistical law, as has been rightly pointed out (Gurwitsch), when regulated growth becomes intelligible only by the assumption of highly probable processes. For since a regulated process of cell division is part and parcel of regulated growth, and since this division leads to quite different arrangements of the daughter cells according to the position of the spindle (cf. the example of the die falling on one corner), the growth of the neural tube, for instance, within the limits of a certain curve would be unthinkable unless certain arrangements of the cells were more frequent than others. But regulated growth is the presupposition of every typical form-growth at the stage of non-functional development [para. 85 ff, 93]. The arrangement of the hairs in hair-groups and the appearance of the first regulated structures in cartilage have to be derived therefrom. Here, too, it merely looks as though the form arose as the result of experiments to discover the most suitable. In the arrangement of hairs in longitudinal rows, the arrangement of scales and feathers, the patterns of stripes and patches, the system of plates in the tortoise-shell, there can be no question of experiment.

Thus, by an analysis of regulated growth, we gain a far-reaching aid to the understanding of inner form (structure). The final analytical step lies in the investigation of the cell forms themselves; they too have a promorphologically definable "form" which exercises considerable influence on the development of structures [para. 97]. Analysis of cell structure would, if it were possible, give us further help.

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(B) Comparison of Form.

Para. 28. As we have already seen, it is only by comparison that the individual form really attains its full significance—indeed, without relation to other forms it has no existence. But every comparison presupposes a comparative principle, just as every measurement demands a scale. We may therefore begin by distinguishing between two principles of comparison, the subjective and the objective. The aim of the subjective principle is to examine the connection in which individual beings are placed with regard to one another by the power of our contemplation and thought [para. 20], and thereby to determine scientifically what are their common features. The objective principle, on the other hand, regards the combination of forms as actually existent independently of us, and endeavours to determine the genetic connections between them. The connection, shown to exist to a greater or lesser degree by the process of comparison of the forms with one another, is termed "relationship." This word is often used to express two entirely different ideas, known scientifically as affinity and consanguinity (Rauther). The two scientific terms exactly coincide with the results of the two methods of comparison, inasmuch as affinity determines relationship according to the form alone without regard to the genetic relations of the formally related objects. In a similar way we speak of related styles in architecture, of related problems in science, related ways of thought of two people. Consanguinity, on the other hand, is applied to relationship in the sense of blood-relationship, and includes the judgment that the beings, which are the bearers of the forms, are derived from one another. That affinity and consanguinity are quite independent of one another can scarcely be assumed ; the connection between them is usually interpreted by making the architectonic similarities the result of descent from a common starting point. We shall examine this later [para. 32]. For the moment we propose to confine ourselves to comparison of form according to subjective principles.

(i) Concept Comparison (Systematics).

The essence of conceptual comparison consists in the elimination in thought of the differences of forms and the retention of points of agreement as systematic characteristics. The forms which agree in a certain number of characteristics are brought together in one class, one systematic category. These categories are arranged in an ascending series : Subspecies, species, genus, families, orders, classes, phyla. In the case of man the first four categories appear to coalesce, and man belongs to the order of primates, the class of mammals, and the phylum of vertebrates.

Two questions which are usually discussed among the principles of systematics should be mentioned here, since they play a part in any consideration of the systematic position of man. The first is that of the "systematic element" (the unit of the system as it is called in a system of currency or weights and measures) ; the second is the question of the reality of systematic categories. The systematic unit selected may be either the species or the individual. Darwin and Haeckel prefer the individual on the ground that since the whole world of forms has diverged by a process of continuous development, the species are mere artificial groups limited by the gaps caused by the disappearance of earlier forms. The formation of unconnected species and natural gaps in the system, such as palæontology teaches us are probable (Jaekel), have caused others to regard the species as the natural element of systematization (Rauther, Jaekel). The species would then be the circle of radiation of very simple individuals related by blood. There are objections to this view, too, since the necessary result is the assumption of the independence of all species and the descent of each from an original multiplicity. For if the species had proceeded from one another, the truth of Haeckel's earlier view would be confirmed. So long as systematization is not separated from the question of descent, it will be difficult to decide between the two views. The probability is that neither is quite correct, because the final element of natural relationship is the genus (Alverdes). From the point of view of pure concept classification the significance of the species as the final concept element ought to be irrefutable, since the species comprises the first more general abstraction standing above the individual, which is at the same time a unity whose members are fertile when crossed with one another, but not with those of other species.

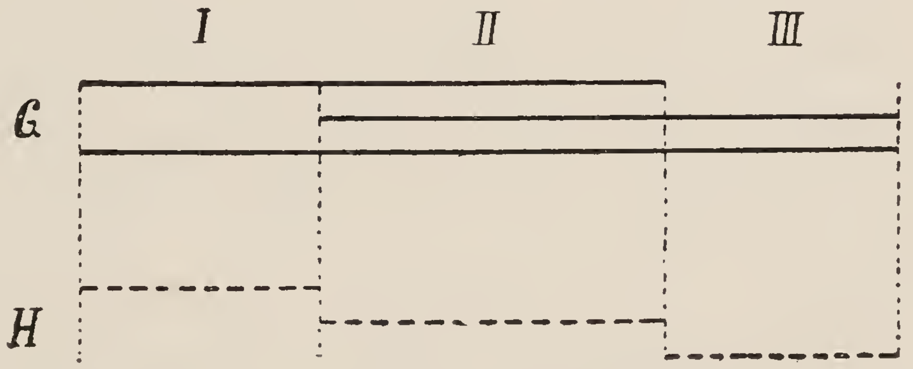
The question of the reality of the categories of the system and of the formal content comprised therein need not by any means involve us in the old scholastic argument about the reality of conceptions or of single forms. For our purpose all that is needed is to emphasize in this connection the peculiarities of the conceptions. It becomes obvious that the conceptual abstraction is a necessity in this case when we note that otherwise any understanding, much less scientific understanding, of the matter is unthinkable. Only by speaking of "beast of prey" or "man" do we escape the impossible task of making every statement with regard to form for all living and extinct individual men; we are thus able to make our statement in such a way that it applies to all men. Conceptual transformation of form is thus presupposed by a certain—not the only [para. 44]—norm-concept, without which any description in natural history is impossible. Something of an empirical-real nature, therefore, corresponds unconditionally to the conception as such. The categories are the conceptual expression of a certain degree of agreement in form between a narrower and a wider group of forms, and are thus for thought what scales are for space and time. This becomes immediately important in the question whether all men belong to a species or a genus, i.e., how we are to estimate the agreement in the form of all men, and consequently the points of difference. And in other respects, too, one may be tempted to ascribe to the contents of a category more than conceptual reality alone. Botanists (Nägeli, Sachs) have rightly pointed out that it is just the higher unities which have first presented themselves to formers of systems, and that older systematization proceeded not from species, but from genera and orders, and that with the progress of knowledge the higher units have been subdivided; the higher group has not been formed from the lower. All this tends to show that in morphology the formation of concepts proceeds from some specific naturally existing state.

It must be carefully noted that the abstracted systematic conception may not be confused with a concrete object. For in actual existence we are presented only with concrete individuals possessing all the individual characteristics in addition to those employed in the diagnosis and the system. It is probable that the species-characteristics pervade the whole individual and exercise a specific influence upon every individual characteristic, so that every individual characteristic is also specific. In the diagnosis of the species, however, we use the smallest possible number of characteristics which will suffice to define the species. The theory of "phylum-forms" was based on the false conclusion that the systematic characteristics were sufficient to characterize a concrete animal. It was forgotten that any such supposed creature, e.g., the "phylum-ancestor" of the mammals or the original ancestor of man (Lemuravus, *Proanthropus alalus*) must also have possessed its individual characteristics, and that we naturally know nothing about them. This is an important argument against the use of phylum forms as genealogical conceptions [para. 46].

In any case modern systematization is not artificial (i.e., not based on one or few characteristics). By using as many characteristics as possible it aims at being the expression of a natural relationship (i.e., at giving an immediate picture of the natural development of the animal world). How far this is accomplished will be discussed later [para. 46].

The whole of the human race now existing is included in one species (*Homo sapiens s. recens*), whose members may all form fertile crosses with one another. Historically this species goes back to the younger Palæolithic age where it first appears as *Homo aurignacensis.* Simultaneously there existed in that epoch in Europe another human form, which as *Homo primigenius* (Neanderthalensis) went back into the older Palæolithic age; the oldest human remains at present known, the Heidelberg lower jaw, are ascribed to a third form, *Homo heidelbergensis* (Schwalbe, Mollison). Whether all these three forms of man are to be evaluated as distinct races or species, whether there is only one species or only one genus, *Homo*, is a question which could only be decided if we knew whether crosses between these forms have taken place. There are certain indications that this is not improbable (Bonnet). In any case the point is not one of paramount importance. In man of recent times the systematic groups have the value of races which may be divided into original or main races (black, yellow, white or European) and races of mixed descent; the latter may then be subdivided into primary, secondary and still younger mixed races.

In all these divisions the category remains in the first instance only the scale and result of comparison. Those men who are brought together into one category possess, in addition to those distinctive characteristics which serve for the purposes of grouping, and which are peculiar to them alone, many others which they share with those in other categories. Black and yellow men possess in common not only those features which serve for diagnosis of race, but also, for example, the form of the brain, eye, femur, etc. We ought really not to speak of single "characteristics"; what determines the race is rather a wide field within which a characteristic may occur. This field may be smaller (e.g., colour or form of the hair, colour of skin, Mongolian upper jaw) or larger (brain form, shape of head), or so large that it covers all races (papillary ridges on the finger tips). Finally, characteristics may even be deduced from the environment (form of head? colour of hair? size? Fischer). In all these cases we have overlapping of the characteristics. Statistically, and therefore conceptually, only those characteristics can be used to delimit a race which belong exclusively to that race. This may be illustrated as follows:—



G = Brain characteristics. H = Skin characteristics. I, II, III = Races.

For differential diagnosis in the simple examples selected here only the skin characteristics can be used. For purposes of classification the brain characteristics would be valueless, because they display no characteristic peculiar to them alone. This applies also to larger groups, e.g., the species. The brain of the chimpanzee shows all the variations (E. Fischer) which occur in the brain of an orang-utang. No distinction between the two anthropoid species can therefore be based on the brain. None the less it might be found on further examination of a sufficiently large number of orang-utangs or chimpanzees that the total extent of variation is greater in the one than in the other, and that, statistically, the most frequent combinations of characteristics of the former differ from those of the latter, or that combinations occur in the one which are also absent in the other. In this way there is always something provisional about all systematic classifications, particularly in the lower series. Border-line species (doubtful species of systems) are familiar. Nothing but an extensive statistical examination of combinations of characters can lead to a decision in such cases, and it should be noted that it is always combinations of characters that should be considered and never individual features [para. 45].

The number of races of man has been continuously increased because attention was drawn to combinations of characters within the larger divisions which were of importance for the systematization of individual groups within the chief races. At first we were content with three or four races (Linnæus, Cuvier). Blumenbach distinguished the familiar five races (white, black, yellow, red and brown, Malay), but these allow of our distinguishing further groups having constant combinations of characters. If we take the smallest number of such combinations by which one group may be distinguished from another, we arrive at twenty-six races. This does not mean to say that further gradations are excluded for the future.

For our purpose, the significant division of European races is that into four chief and six secondary races (Ripley, Günther). This division already plays a part in anatomical studies. For although it is true that the bodies studied in our dissecting rooms are the outcome of complicated crosses between the races, yet these crosses will produce widely different products in different dissecting rooms, because, for instance, a cross, A × B × C, such as is, perhaps, common in the East, resulted in a different final product from the cross, B × C × D, such as is most usual in the West. These final products we call populations. It is, for example, well known that the thorax of the North German population differs so decidedly as regards the position of the ribs from that of the Swiss, that the anatomist who goes from one population to the other has to revise his knowledge of the thorax.

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(ii) Formal Comparison.

Para. 29. From this mental conception, which through ignoring differences of organization proceeds in this intellectual way to the erection of categories, there is distinguished through the synthesis of such ideas a result which is not non-conceptual, but belongs altogether to an abstract generalization, viz., the erection of types. This is never an individual, however near to the type an individual may sometimes be, but always something actual, which exists only in the abundance of numerous individual examples. We might put it differently—and it would be more than a mere change of words [para. 42]—by saying that a gigantic game of combination had been played and that the possibilities of form were only exhausted with the total of all possible combinations of throws. This possibility is not unlimited, but varies within moderate limits, and for this reason it has been regarded as the first task of comparative anatomy since the time of Goethe and Gegenbauer not to examine one individual, but to bring together systematically all possible variations of one form.

Goethe devised a scheme for this (Lubosch), according to which work was to proceed to actual practice. He wrote the parts of the skeleton one below the other in a column, the animals one beside the other in another column, and wanted to fill every space in the figure by systematic investigation. This can naturally not be carried out to the last detail, but none the less Gegenbauer, the founder of modern comparative anatomy—and his pupils have followed him—has never forgotten this principle, as may be seen from a study of his textbook.

In all this it is the variations of the organization which recede into the background in systematic comparison, this being the chief purpose. The variation may be one of number (ribs, vertebræ, carpalia, tarsalia, measure, weight), or of form and position (heart situated cranially in fishes, caudally in the thorax in mammals; the brain above the nasal capsule in mammals, behind it in man; position of the fins and extremities with regard to the vertebral column, etc.). All these variations are united to form a composite picture, so that not only is every individual organism represented with all its characteristics, but the complex of all individual organisms becomes in our imaginations a superindividual unity. Empirically expressed, "the mammal" would not be the abstract idea of systematization with its five characteristics (hairy, viviparous, mammary glands, temporo-mandibular articulation, corpus callosum), but the superindividual existence of all living and fossil mammals simultaneously summoned before the eye of the imagination with all their characteristics of number, order and position. Larger and smaller groups of forms may be thought of in the same way. The composite pictures obtained in this way are termed types. Such a type shows not only the smallest number of differential characteristics common to the group, but also embraces everything else occurring in the group. Thus the ideal type of the mammal has, as common features, the ground plan of the structure of the skull, the common characteristics of the skeleton and musculature, and also at the same time in its individual members all the variations of numbers (e.g., 12, 13, 18 ribs), of form (e.g., the single-chambered heart, lobed and simple lungs, and those provided with marked increase of surface), and position (e.g., position of the heart, of the pleural cavity, of the diaphragm, of the gonads, etc.), which have ever appeared in individual forms, and that in such a way that an organ can show, at one and the same time, agreement and variation, e.g., the foot, hand, arm and wing. If all the individual forms of a type are compared, we get, therefore, in addition to our recognition of permanence in the type, an impression of change, of movement. The old school of comparative anatomy gave to this apparent movement within the type the name of metamorphosis. We may admit this term within modern science without objection, particularly as a contrast to the actual change of one form into another, which we call transformation [para. 31]. Type and metamorphosis have become the starting points of the scientific comparison of organic forms, and therefore they possess an importance for human anatomy too, which can scarcely be overestimated. We therefore discuss here the underlying principles, while their practical application will form the main part of the special morphology of man in a later chapter.

The value of all this for human anatomy may be seen from what has already been said. For if we really succeed in subordinating the human organization with regard to number, form and position of its organs, and in following within this type the metamorphoses which have led up to the human form, we shall then gain an insight into what is termed the plan of the body, a term which may be and often is misunderstood. Turning now to the principles of formal comparison, we have first to treat of the type and then of the metamorphosis.

Our task in examining the type rests really on the determination of its limits. These lie at the spot at which the occurrence of some organ, formally of equal value, is no longer demonstrable.

For example, a chorda dorsalis, or an optic cup from the brain, are demonstrable beyond the vertebrates only in the tunicates. In a very wide type both Tunicata and Vertebrata would thus have to be included. With every organism we therefore have to ask how far one of its elements corresponds to one of like formal value in other organisms? To the superficial critic the answer to this question seems very easy, since he may imagine that it is easy to tell at sight whether organs are of like value or not. In reality the question is a very difficult one and demands far-reaching anatomical study. It has already been pointed out (page 22), that that which performs a like function (e.g., hind-gut of amphibians and hind-gut of mammals) must be distinguished from that which is of like form; we must decide whether the hind-gut in mammals corresponds to any part of the alimentary canal of like value in the non-mammals, or whether, perhaps, in their case, the functions of the hind-gut are performed by what in mammals is the small intestine. Organs of like formal value have been called homologous (Owen, 1848), a term which has become general (cf. Spemann, Peter, Lubosch). The difficulty in determining homologies lies in the fact that homologous organs are often extremely unlike in form, and may perform quite different functions. For instance, the hair sheaths of man are of like formal value with the epidermal sheaths around the sense organs of the skin in the amphibia (Maurer). We might not think that the styloid process, the stapes and the cartilage of the external ear are homologous with the second visceral arch of fishes, or that the muscle elements of the diaphragm are homologous with muscles which in the amphibia and reptiles are situated in the cervical region. The investigation of homologies is thus the method which without regard to function brings formal order into the organism, not by introducing it artificially from without, but by bringing to light by means of comparison the order already hidden there.

By what means the homology of two parts may be determined is an important and extremely difficult question. The older morphology was satisfied with the test of position alone. The determination of homologies followed immediately from the application of the *loi des connections* [para. 27]. And this to-day is the first, and in many cases an adequate means. Thus all vagus nerves are homologous; similarly the spiracle and the middle ear are homologous, that branch of the facial nerve which runs from the posterior to the anterior wall of the spiracle, or of the middle ear on the medial aspect of the lower jaw in non-mammals (the malleus in mammals) and the third branch of the trigeminus (chorda tympani) are homologous. Homologous are the nervi laterales vagi of the fishes and the ramus auricularis vagi of man, the sinus venosus of fishes and part of the right atrium in man. On the other hand, the arteria brachialis (anterior) of many mammals situated in front of the median nerve, and the arteria branchialis of man behind this nerve, are not homologous.

But in other cases the determination of position no longer suffices to-day, because the development of the body is accompanied by far-reaching alterations in position, particularly, for instance, in the musculature where the nerve connection forms the only criterion of homology. This is also the case with the homology of the opening of the pronephric duct and the ostium abdominale of the Fallopian tube, so that many homologies were falsely set up in earlier times or not recognized at all.

Thus St. Geoffrey Hilaire taught that the auditory ossicles of man and mammals were comparable to the operculum of fishes, while embryology has since shown that the bones are homologous with the components of the articulation of the lower jaw of non-mammals.

The urinary bladder of all amniotes considered solely in regard to its position appears always to be a homologous organ, while embryology shows that it is not of precisely the same value in the individual classes and orders, because the opening of the Wollfian duct is included in the formation of the bladder in some cases, while in others the urogenital sinus alone forms the bladder (Felix). The gills of fishes originate from the entoderm (they are internal gills) in contrast with the external gills of amphibia which are produced from ectoderm, and the various gill formations are not homologous. Modern methods are therefore not merely concerned with position in the developed form, but also with the position in the embryo. And since, as we go further back, the position in the embryo can be traced back to the cell groups in the germ layers, we arrive at a genetic formulation of homology, according to which things of like origin are homologous, e.g., what originates in the same parts of the germ layers, branchial grooves (thymus, parathyroids tonsils), or from like areas of the small intestine (liver ducts, pancreas primordium).

Speaking generally this may be regarded as no chance definition, for the organs which we prove as homologous are known to us only in the adult state. This is followed back until we finally conclude that what is of like origin is homologous.

It may be added that the like origin is frequently obscured by embroyonic displacement and submergence of the segmenting material, so that, for example, the chorda dorsalis, the complete homology of which can scarcely be doubted, originates in some animals in the entoderm, and in some, at any rate in part, from the mesoderm. A difficulty in the study of homology is presented by the question of thymus in mammals (Peter); this originates for the most part from the entoderm of the branchial grooves; in the mole from the ectoderm of the sinus cervicalis, in the pig and the guinea-pig from the ectoderm and entoderm. The structure of the developed organ is, however, the same in all cases. The case of the blood-islands is somewhat similar, for these have their origin partly in entoderm and partly in mesoderm, and yet as a whole are to be regarded as a system of like formal value. These displacements of cell material also occur at later stages of embryonic development and render it impossible for us to base the homology upon like origin. For example, the trunk musculature (rectus and oblique ventral muscles) originates in many mammals without demonstrable connection with the ventral myotomes, while in fishes, amphibia and man (Zechel) this is quite clearly its origin; but we should be wrong if, because of this, we regarded the ventral muscles of mammals and non-mammals as not homologous, for the topography of all adult forms shows these organs in complete agreement (nerve connections, origins, connection with adjacent organs). We may therefore say that the origin could only be regarded as the foundation of homologies if we were acquainted with the whole of the alteration of the cell material, from the segmentation to the primordial cell groups in every detail, which is not yet the case. If we had this knowledge, then the homology would be traceable back to the ultimate elements, and the ultimate object of the investigation of homologies may be defined as the effort to trace the organs back to the homologous formation areas of the earliest embryonal stages [see immediately below and para. 91]. Here we have the proof of our statement made above, that in investigating homology we find many cases that are not only extremely difficult to solve but at present insoluble if proof of common origin is demanded.

Some few particularly difficult cases from the theoretical standpoint may be mentioned here. By the term imitative homology (Fürbringer) we understand the relation of two organs which are undoubtedly of like formal value, but occur in different positions. Parts of the human skull or the clavicle are rigid substances in the integument on the first appearance in the fishes (bone scales). This is expressed by saying that the dermal skeletal parts assume in the course of development a deeper position, and come into relation with the cartilaginous skeleton. If we assume that it is different cell elements in the two cases, those of the horny skin in one, those of the perichondral tissue in the other, which form organs of like value (e.g., the basal plates of the teeth of fishes and the membrane bones of the mucous membrane like the palate, and the vomer), then we might say that in mammals the formative cells imitate the skin organs (hence the term imitative homology). This is, however, not quite certain, since proof is naturally wanting that the formative cells of the clavicle do not reach their position by extensive displacements [para 91]. The word "imitate" assumes a certain conscious cell activity, and thus merely provides a name for the process of cell displacement in the embryo which is actually unknown to us, but which is comprehensible, even though we cannot see its whole working, even in the simpler cases such as the chorda and the blood-vascular system. Organs which are completely homologous in position, structure, and origin, are also termed homogeneous; those which are homologous in position and structure only, but probably, or at any rate, not demonstrably so in origin, are termed homoplastic (Gadow, Braus). With our present knowledge it may be said that most homologous organs are homoplastic, or at least that it is not clear that equivalent organs, e g., the liver, cannot none the less originate in different parts (Jacobshagen, 1927, p. 39), The results of experiments to determine homology are naturally of little value (Peter) because many cells are capable of producing experimentally what they do not normally produce.

The determination of homology is always based on the normal development and the comparison of normally developed organs. But here, as long as we have no recognized methods, we must depend upon the test of implantation and explanation (Braus) in order to distinguish microscopically between the cell stems, particularly in the mesenchyme, and to follow their movements. Since the decisive processes take place in the invisible differentiation, this is at present our only means of investigating those differentiation processes which precede the visible differentiations.

To sum up, we may say that deduction from the same position is generally regarded to-day as the most significant methodic means for determining homologies (Lubosch, Jacobshagen, Peter, Naef). To base them upon origin from the same material soil is by some held to be fruitless, and is rejected as a method for the investigation of homologies (Jacobshagen), by others regarded as necessary (Peter, Braus, Lubosch), and applied either to the visible primordium (Peter) or to the invisible (Braus, Lubosch). Experimental methods are advocated (Braus), or the necessity of examining the differentiation and variety of the cell material cytologically [see below, para. 91]. Without this knowledge of the as yet invisible development, exact determination of homologies is at present often impossible. In every case of doubt the test of position must, as far as possible, be traced back to the ontogenesis.

The term allomerous homology (Jacobshagen) is an important enrichment of our world of conceptions and judgments [para. 5].

For it cannot be said without qualification in what homologous relationship a rib or a vertebra of man stands to the ribs and vertebræ of a frog, which possesses far fewer than a man. And so with many other organs. Here we might recall the fœtal membranes. The embryonic membranes of amniotes originate in the ectodermal covering of the yolk sac in fishes with meroblastic segmentation. Are they homologous without further qualification? The outer covering of the yolk sac is of the same value as the ventral abdominal wall of amphibian larvæ. Are then the placenta and the amnion homologous with this area? In the amphibia and mammals there lies above the amnion a particular layer [trophoblast, para. 77, ff]. The sense organs and the nervous system which in fishes and reptiles originate from the whole thickness of the ectoderm are produced in amphibia and mammals from the basal layers only. Then are the sense organs of all animals completely homologous? In amphibia each of the cells of the first division forms one half of the developing embryo, in mammals one cell produces only a small part of the embryo; from the other comes the whole of the body, together with the fœtal membranes. Strictly speaking, the whole mammal (without the fœtal membranes) would correspond to only part of the body of the frog (Peter). In all these cases we must take into account the processes of growth and the production of complex derivatives from simple primordia [para. 86], and cannot describe simply as homologous the many parts corresponding to the fewer original ones. The term allomerous homology is in such cases a distinct improvement.

The older morphologists distinguished two kinds of homology in organisms; those respectively of equivalent elements within the same organisms and one and the same element in different organisms. The former was general, the latter special homology.

The latter sort alone still retains the old name, while the term homodynamy has been introduced for special homology (cf. Gegenbaur, Lehrbuch d. vgl. Anat. Einleitung). And this is quite right, inasmuch as the situation then to be considered differs from that which we have been discussing hitherto, and is one which is repeated a number of times in the body, so that we are not comparing various organisms from the standpoint of this characteristic but different areas of the same body.

Homology (= the older special homology) embraces those organs and parts of organs which are formally equivalent to one another in different organisms. We shall add no further examples here to those already given above. Difficulties arise when the organs are not completely, but only partially, homologous; thus the urinary bladders of mammals, birds, amphibia, and reptiles are not completely homologous. Some include more parts than others. The fact is that every part of a form must or can recur in others—and this has frequently been the source of new discoveries just as the existence of planets can be postulated by the astronomers. By filling in the above table of Goethe, which may be done for every characteristic and for every group of forms, it may be seen whether, how, and in what manner and combination the individual organs are present in each individual organism. Whatever is wanting may then be sought. Often it has been discovered, e.g., the nerve of the fifth visceral arch in man. That Goethe, if he did not actually discover the premaxilla, did at any rate determine that it was a typical component of the human jaw, is a familiar fact.

Homodynamy has a difficult but not less important connection with form. While special homology is concerned with the same element in different organisms, homodynamy deals with like elements in the same form. Since the element is found arranged serially, homodynamy is termed serial homology. This phenomenon is apparent to anyone who examines the vertebral column and may be easily perceived in many other parts of the body. The scientific object involved is the determination in what organs this serial connection exists and to what degree the same element lies concealed under various disguises in various organs of the body. Thus we recognize the type of vertebra in the cervical, thoracic and lumbar vertebræ and in the vertebræ of the sacrum and the coccyx, and in all these regions we find ribs or their rudiments. We see the same in the trunk musculature of the body, in the nerves of the trunk, in the branches of the aorta and in many internal organs, e.g., those of the urogenital system. In the head the visceral arches, the organs of the branchial grooves, nerves and arteries of the head display similar homodynamies. Of special importance is the examination of regions which appear to possess no connection with homodynamic elements, and for that very reason cause us to ask whether elements cannot be shown to exist in them which are already demonstrable in other areas. Thus we have the question of the development of the skull from vertebral elements or the derivation of the extremities from other known parts [para. 67 ff]. The elements of the skeleton, muscles, nerves, vessels and many other components of the trunk are disposed in like relation to one another serially in a craniocaudal direction in such a way that we get entire sections (segments, metameres), each of which contains all the elements in constant relation to one another. The homodynamy of our body thus finds its pre-eminent expression in its metamerism, the investigation of which has thrown much light upon the normal understanding of the body [para. 51].

Para. 30—If we now glance at a large number of organizations in which we have established homologies we shall see the same organ in widely different forms; and if we apply ourselves to the structure of one and the same organism a small number of elements show throughout the body an overwhelming abundance of variations of form. To the mental eye they appear in a state of flux (Gegenbaur); we get the impression that the multiplicity of forms in which vertebrates appear rests less upon new formation than upon an inexhaustible transformation of the same elements. To this apparent change of organism we give the classic name of metamorphosis; and just as homology is distinguished from homodynamy, so also we differentiate special from general metamorphosis.

Simultaneous special metamorphosis is the term applied to the transformation of the same organ in different animals (cf. p. 74 and fig. 3). This transformation may be one of form or one of position or of a combination of the two. If we take the system of the anterior extremities we find their primitive elements in the pectoral fins of fishes. The fin is metamorphosed into the terrestrial extremity by displacement of its parts, by loss of certain portions corresponding roughly to the phalanges, metacarpals and carpals, by the addition of bones which are originally present as dermal skeletal elements. We can trace then exactly the development of the individual bones, the scapula, coracoid, clavicle, humerus, ulna, radius, the ten carpals, etc. The extremities may be used for swimming (aquatic reptiles and mammals), flying (birds), digging (moles), climbing (marsupials, lemurs, apes, man); it is always the same primitive elements from which Nature, as from plastic material, has formed a diversity of apparatus suited to all manner of uses without, as it were, the ability to add a new component to the system. With all the organs the facts are the same. Additional elements may be found in the skull which once belonged to the trunk, the urinary organs unite with the genital and permit certain of their elements to form parts of other organs (e.g., the pronephros, the ostium abdominale of the Fallopian tube). The single organs, however, appear not only to undergo transformation but also to alter their position.

They appear to become displaced. In primitive forms the heart lies close behind the head; then it appears to move in a caudal direction; the ventral fins seem to move forward, the upper extremities to move further back and the hind ones towards the front.

A further aspect of simultaneous special metamorphosis is also important. Its phenomena received their first and fundamental description in Goethe's Metamorphosis of Plants. The view here adopted was that one and the same element, the leaf, is metamorphosed into all the component parts of the plant: calyx, petals, stamens, that the plant is in fact the leaf. This has often been misunderstood (and Goethe himself contributed to the misunderstanding by his terminology) to mean that the plant was originally the leaf in the literal sense, and that petal and stamen are then developed via the leaf. It is, however, quite clear that Goethe did not intend us to understand him in this way (Lubosch). From the standpoint of embryology, we may say that wherever a pollen-thread appears the primordium of the leaf develops at once into the stamen tube, not first into a leaf. Something of the kind does actually take place, for the "vertebral theory of the skull," which is based upon similar considerations, has found its vindication in this sense. It is not the developed vertebræ which are transformed into bones of the skull, but the primordium from which, in the trunk, the vertebræ are developed. It forms, in the region of the head, portions of the base of the skull (parachordals, Huxley). The same question arose in the study of the comparative anatomy of the extremities. Attention has been drawn at an early date (K. E. von Bär), to the homodynamy of the shoulder-girdle with the bones of the jaw. Later, comparative anatomy recognized a homodynamy in the fins and extremities and the visceral arch and proclaimed the metamorphosis of the visceral arches into the limb-skeleton [archipterygium theory, para. 67]. It was believed that here, too, a movement of the extremities from the region of the head to that of the trunk had taken place.

This idea, as such, is an extraordinarily fruitful one, for it enables us to grasp with our minds the inconceivably wonderful fact that front and hind extremities proceed from almost the same original component parts. For it is obvious that the humerus corresponds to the femur, radius and ulna to the tibia and fibula, the ten carpalia to the ten tarsalia, etc., the N. medianus and N. ulnaris correspond to N. tibialis and N. peroneus; and the muscles of hand and foot show many common features. It is just this which explains why all attempts to derive the front extremity from the hinder or vice versa are in vain. The special anatomy of the muscles, nerves, vessels, and even of the bones, opposes insuperable difficulties to any such derivation [para. 70]. The seven surviving carpals do not correspond to the seven definitive tarsals, there is no adductor and peronal musculature in the arm, no M. opponens pollicis in the foot; the system of arteries is quite different. The truth here is, as it was in the case of the vertebræ; the lumbar vertebræ have never been actually transformed into thoracic and cervical vertebræ or into bones of the skull, nor has a hind extremity ever been actually transformed into a front one, but like serial homologous, homodynamic elements have developed differently in different areas of the body. It is from this that the appearance of metamorphosis arises.

What has been said is true also of the form of the body as a whole. It was Petrus Camper, as Goethe tells us, who drew an animal on the blackboard and transformed it with strokes of the chalk, first into another animal and finally into man. There can be no doubt that the first point here is the employment of the principles of special and general metamorphosis, but for the whole body something else, something more real is added. At this point, knowledge of homology, constant topography [para. 27] appears, setting definite limits in the proportions of the whole organism to all displacements of the parts and their changes. To this reference has been made already (p. 87). The figure there given and its explanation may serve to explain what Camper put forward 100 years ago. Here we have proof that transformations of organisms in nature actually follow laws which are the outcome of internal, topographically fixed relationships among the elements which undergo metamorphosis.

We have here set forth only the general principles of formal comparison. The results of the application of these principles to human anatomy will form a main part of our later pages.

Theoretical, systematic, comparative methods enabled us to place the individual man in his correct position in relation to mankind in general and to the animal world. Formal comparison based upon types now makes it possible for us to convert that stiff theoretical system into the phenomenon of multiform life. Its characteristic is the vast abundance of forms coupled with a simplicity and limitation which yet never becomes machine-like. The layman will see in organisms only the differences; the morphologist perceives that in reality there are only similarities, and will note how the whole multiplicity of animal forms develops from a comparatively small number of elements. This is true in the case of man, and it is the task of scientific anatomy to demonstrate this truth.

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(2) Ætiological Considerations.

Para. 31. Up to this point we have concerned ourselves with forms without troubling ourselves whether they may change in size or not. As soon as we neglect this point and inquire as to their capability of change, its degree and extent, morphology alone is no longer competent. Every change (transformation) requires a proved cause and definite stimuli [para. 21]. We shall now attempt to gain a general view of the present position of the theory of transformation, and thus to approach the problems which that theory sets us; we shall then discuss the causal foundations of transformation, and finally, we shall deal briefly with the various hypotheses.

(A) Transformation; Introduction; Phenomena and Problems.

Transformation of forms is an actual fact. We see the process at work in the development of every living creature. And the sequence of forms of which an individual life history, from the fertilized egg-cell to the dying organism, is composed, is connected within itself by a causal chain, as it is with the life-histories of the parents. Pure description of the successive forms is of great value for knowledge of individual development, but throws no light on the forces which govern them. Processes of transformation in fully formed organisms are also not unknown. Acclimatization shows us in man, animals and plants far-reaching changes accompanying fresh environment (man in the tropics, Alpine plants in the plains, etc.). These influences of environment may even extend beyond the limits of one generation, for we know, for instance, that the children of Europeans who have emigrated to America show variations from the somatic type of the parents (Boas). Experimentally, too, permanent changes in subsequent generations can be produced (butterflies, beetles) by causing certain influences (heat, cold, hunger, etc.) to act upon the parents at a certain time in the formation of the sex cells. And we know that the formation of species actually takes place to-day, as, for example, when a species of fresh-water fish taken from a lake and transported to a new environment produces in its new home a generation so different that we are obliged to call it a new species (Thienemann).

But these few facts, certain though they are, by no means suffice to corroborate that theory which Lamarck maintained as early as the beginning of the nineteenth century, and which later, under the guise of Darwinism, regarded all living organisms as links in a great continuous transformation-chain, and developed the idea of descent of the higher [para. 16] from the lower forms. This hypothesis is obviously of no small importance for anatomy, for if it be a fact that organisms are derived from one another by a process of form change, then man is not excluded.

If we demand proof of the causes that millions of years ago animals have been transformed, we are setting a problem both senseless and insoluble. For cause and effect can only be established for something present. The problem is rather to observe or produce in the laboratory, though it be only once, an actual inheritable transformation of an extent such as the theory of descent demands (e.g., a first chicken). Then we should be in the position to assume, at any rate in principle, a similar process for the past. So far the process is a hypothetical one, since we can make the connection between the forms intelligible in another (see below) but not in any better way. The gravamen of this limitation does not lie in the historical aspect, for we accept historical processes as completely justified, although no one living to-day was present when they took place. Just as we deduce from archæology a Babylonian tower, the seven Trojan settlements, the plans of towns of the Stone Age, and so on, we are also at liberty to deduce the process of transformation without logical errors from the existing evidences of palæontology. The difference between historical morphology and the history of man —leaving out of the question other factors which play a part— consists in the fact that we may transfer motives and phenomena with every right from the present history of man to the past, while for historical morphology at present we are ignorant whether what we believe ourselves able to explain by means of the transformation theory has not actually come about by quite other means. It is quite conceivable that all existing species have followed their own paths of development, starting from primitive forms of life (single-celled forms) which were similar to one another but constitutionally as different as the later species. This was roughly Bonnet's view, and is still the view of many theorists. A ladder of this kind, with steps differing infinitesimally from one another, would show a picture of historical forms such as we have before us.

The task of historical morphology with regard to the transformation theory can therefore only be: (1) To create or prove heritable transformation in some way or other; and (2) so long as that is not possible to get theoretically clear as to the processes which must take place in organisms if their transformation is to be possible. The first point contains a methodologically unavoidable demand, which is the object of all experimental genetics. The demand is not altered by pointing to the shortness of human life and the length of time necessary for transformation, for surely some process of transformation, which has been in train for countless years, must be brought to an end within measurable time. Yet nothing of the kind has ever been observed.

Thus Darwin's hypothesis has in recent times suffered the peculiar fate of finding it more and more difficult to verify its fundamental assertions by observation. In essential points it has suffered limitations and even refutations. Not often has science found itself situated as it does to-day towards Darwinism. All appearances certainly speak convincingly for the transformation and descent of forms, but we know no influence of any sort which must necessarily bring about such transformation (Alverdes); granted that we know of modifications which change organisms, yet they do this "blindly," and not so that something "adapted" to the environment should arise therefrom. And, above all, this does not take place to the extent demanded by the Darwinian theory which here assumes in some way or other "regulated chance" (see above), by stating that descendants show in their variations just such differences as are suitable for cultivation. It is also out of the question to say that the infinitely complicated apparatus of a mammal, for example, has arisen through gradual cultivation, for we can imagine no time so long and no circumstances so complicated as to be capable of transforming one organism into another in this way. Further, we now know that organisms are not spontaneously changeable by inheritance but are constant, and that those changes, which we produce artificially or can observe as spontaneous, to-day at any rate do not lead to the formation of species. All this admits of one conclusion only, namely, that—if the formation and transformation of species has ever taken place at all—the forces productive thereof are either quite unknown to us (Alverdes) or else the effect of known forces has taken place under conditions of environment which no longer exists.

The latter is not very likely, for the Interglacial ages in Europe to which we refer important changes in the human race were accompanied by climatic conditions which exist to-day in subtropical regions, and yet these do not lead to a change in man, let alone any inheritable transformation.

With regard to the Darwinian theory then the position is that we certainly now possess methods for investigating how and under what conditions lasting changes may occur in organisms, but that these methods are not applicable to the objects the historical transformation of which is asserted by Darwinism [para. 35]; further, that the formation of a new species cannot be produced by any exact method but that none the less we cannot doubt the ability of species to alter. Palæontology compels us to believe in this ability, by showing us mammals coming later in the earth's history than amphibians and man later than the mammals, so that we are forced to seek the precursors of the higher forms among the lower. The advance of the theory of descent consists in the fact that we are to-day in the position to treat causally the question of the ability of organisms to change. This is the task of the experimental investigation of inheritance; for if we know what cause leads to the change of a form, then we are at the same time able to conclude that such causes have in all probability played a part in the transformation of species. What we do not know, and can never learn, is whether these causes, which we are now able to produce artificially, have alone been effective, and under what conditions they have occurred. Darwinians did not at first reflect that they were treating a causal problem such as is presented by transformation of species, without being able to attack it scientifically from the causal angle.

(B) Causal Principles of Transformation.

Para. 32. Everything which can be said with certainty about the causes and conditions of the transformation of organisms can be brought within three chief principles: (1) The constitutional principle, as the primary one, stands above all others. This principle declares that the given germ-plasm is decisive for everything which proceeds from it. The germ-plasm is the real "cause" [para. 21 ff.], the effect of which is the formation of typical shapes and proportions, specific structure, texture and typical cellular microscopic structure of the organism. Only a permanent change in this given constitution of the given germ-plasm can result in the origin of another organization. The transformation of one organism into another is therefore inheritable transformation of the germ-plasm constitution. (2) Next comes the principle of partial selection (functional adaptation), which, on the basis of a germ-plasma constitution capable of adaptation, causes something immediately adapted to originate within those limits in which the reaction capability of the germ-plasm lies. And (3) there is the principle of personal selection (Darwin's selection) which preserves the adaptable germ-plasms. To the first of these principles we shall devote a somewhat more detailed, to the others a brief consideration.

(i) The Constitutional Element and its Changes as the Cause of Transformation.

The term germ-plasm indicates the living substances present in the ripe spermatozoon and the ripe ovum, which serve for the preservation of the parental characteristics; and here we use the term without regard to the structure of these substances or to their locality in the cells, i.e., we are taking them here in the genetic sense only. As the result of fertilization the parental germ-plasms come into certain quantitative relations and thus form the germ-plasm of the new being, the "species cell" (O. Hertwig), the "original whole" (Kraus). It contains implicitly that which forms the constitution of the being (Tandler). Thus, according to what we have said above [para. 21], we have the right to regard this germ-plasm as the cause of individual development and forms, because it represents that state as the result of whose change a new state, the two-cell stage, and later, the whole germ development, arises. For the same reasons, if from a germ-plasm a different germ history and a new form are to rise, we must necessarily assume a different constitution of this germ-plasm, i.e., preceding change in its inner nature. Such a change must, therefore, be considered as a cause, further removed and at present the ultimate imaginable cause, of a transformation.

The exact science of inheritance has adopted the term "genotype" for the primordia, unchangeable in themselves, present in the germ-plasm, but the developed being does not bring this genotype before us as a visible phenomenon, because the environment so influences the germ-plasm and its products, the cells, tissue organs and the whole organism, that, in spite of similar and to a large extent coincident genotypes, various forms arise, or the same form assumes different features under different external conditions. Thus water and ice are forms of the same chemical body, and in a flower which has a red bloom in one temperature and a white in another it is impossible to recognize the genotype; we can only say that the genotype contains primordia (genes) with the capability of developing blooms which assume colours differing according to the temperature.

Since organisms are to the greatest possible degree under the influence of the external world, we cannot draw conclusions as to their appearance from their primordia, nor vice versâ, without further consideration. The appearance of a being is therefore termed the phenotype. The genotype H_2O possesses the phenotypes—ice, water, snow-crystals, etc.

If Ph stands for the phenotype, G for the genotype and R for the stimuli of the external world, we have the following formula :—

$$Ph = f\,(G.\,R),$$

which means that the phenotype is a sort of mathematical function of the joint effect of genotype and external world conditions. To avoid any misunderstanding, it is necessary to utter an emphatic warning against taking this formula as an explanation. It merely represents symbolically a fundamental, causal and conditional relation ; but the symbol has the advantage that we can conveniently discuss it as a formula from every point of view, and can thus get a mental picture of the share of causes and conditions in the appearance of organisms.

Let us consider first the influence of various external conditions upon a given organism. They may be introduced into the formula by means of R ($Ra, Rb\ .\ .\ .\ Rn$). We should then get a corresponding number of differing phenotypes provided that the germ-plasm permits of reaction to all the variations of R.

Thus we get the forms :—

$$Pha = f\,(G.Ra).$$
$$Phb = f\,(G.Rb).$$
$$Phn = f\,(G.Rn).$$

These varying Ph are termed acclimatization "variations of locality," somations (because they affect only the soma, not the gene of the sex cells). The cause of all these Ph is always G, which under the influence of the various R is capable not of unlimited but of very widely differing reactions. The essential point of these reactions however, is that they are concerned only with the individual, never with the descendants. If Pha is put back to R, it becomes Ph again, and if Pha begets descendants they will always come into the world as Ph. If the descendants develop under Ra, they may possibly retain Pha. From Ra, Rb, etc., Rn, a new species of constant inheritance can never arise.

If G becomes G^1, things are different. Then we have :—

$$Ph^1 = f\,(G^1R).$$

This is a new species of constant inheritance. The same changes in point of detail may take place here, since

$$Ph^1{}_a\ .\ .\ .\ {}_n = f\,G^1R_a\ .\ .\ .\ {}_n.$$

If we imagine within G a complex of genes, possessing under the influence of the moist element Rw the ability of adapting themselves to life in the water, and if we write this in the form $G(+G_w)$, then we get

$$Ph_w = fG\,(+G_w).\,R_w.$$

(e.g., marine reptiles). The same G_w can be imagined as given by the course of inheritance to numerous other forms. Then mammals, too,

$$Ph^1_w = fG^1\ (+G_w).R_w$$

would possess the possibility of becoming marine creatures, e.g., seals (carnivora), beavers (rodents), cetacea (ungulates), while others according to the formula

$$Ph^1 = f\,(G^1R_w)$$

overwhelmed by environmental factors without the ability of transformation would perish. Between Ph_w (sea reptiles), Ph^1_w (marine mammals) and Ph^2_w (perhaps bony fishes) considerable similarities in body form could then exist, ($Ph_w \sim Ph^1_w \sim Ph^2_w$, so-called convergence), while upon the difference of $G,G,^1G^2$ would rest the extraordinarily differing organizations of these marine creatures. The similar organs could be analogous without being necessarily homologous, e.g., the caudal fins of fishes and the tail of a dolphin.

The cause of the origin of an organization adapted to marine life thus lies not in the external circumstances, although they too are necessary to the formation of this organization, but in the peculiar constitution of the germ-plasm. And accordingly the cause of the development of man from pre-human forms will lie in the presence of a peculiar "man-G." For the tranformation of organisms, and the new formation of species the task of causal investigation thus consists in examining how G^1,G^2,G^3 are derived from G.

Before the appearance of Johannsen's work the older "transformists" were not in a position to face this task, for the exact science of inheritance has only more recently succeeded in establishing its principles. This science provides the only causal method of investigating a phylogenetic transformation of organisms. We now know with sufficient certainty that G is remarkably constant, but that under certain circumstances external influence may succeed in changing G into G^1; and, further, that under certain conditions, even in quite pure stocks, such changes might occur of themselves. These changes are not of the kind which we should have to presuppose if we imagined, for instance, the transformation of an amphibian into a mammal. For our artificially obtained or spontaneously occurring inheritable changes of the genotype affect only subordinate features (colour, hair, decrease or increase of fingers and toes, altered proportions, e.g., of ear length); they are thus quite "blind" and bear no relation to "adaptations." Only a part of these mutations, the so-called "loss mutations," may possibly possess phylogenetic significance. Spontaneous occurrence of inheritable hairlessness or loss of pigment is noticed in the breeding of animals. It is conceivable that lack of hair in man, the whiteness and blondness of the European races, the minimum number of fingers and toes (hoofed animals), degeneration of the teeth and decrease in their number may be explained causally on these lines.

The inheritable variations of the germ-plasm are divided into idiovariations and mixovariations (both together are called blastations, Prell). Idiovariation is the process which in earlier times was called mutation in the narrower sense and is the name given to a transformation in the constitutional character of the germ-plasm taking place under the influence of unknown pre-factors, external or internal. It is probable that at certain stages of their growth the germ-cells are particularly receptive of alterations (Lubosch) and react with a change of G. Such changes appear phenotypically in the occurrence of hairless or albino animals in experimental breeding. When, however, new combinations of features characterized by constancy appear among numerous inconstant ones in bastard crosses, then we have mixovariation. This is governed by the familiar Mendelian numerical law. In crosses of parents differing from one another in characteristics, 2^{2n}, different combinations of characteristics can occur in the grandchildren; of these, 2^n are so-called homozygotic new combinations, i.e., in pure breeds they no longer tend to differentiate. Both kinds, idio- and mixo-variations may occur together, when the sex cells of one parent have already been changed by mutation and their combination with those of the other parent thereby assumes the character of a bastardization (Klebs). The important thing for the whole question is that all the new characteristics arising from the change of G are inheritable.

We shall say something elsewhere of the interpretation placed to-day upon the finer processes of these changes in the germ-plasms. Here it need only be said that, according to all we know at present, the changes appear always to occur singly, in a single individual. Any transference to evolutionary history, therefore, requires some auxiliary hypothesis (cf. Plate), because it is not easy to imagine that a single individual of changed form could have been assured of survival and could have formed the starting point of a new species.

If we transfer inheritance logically to hypothetical processes in the formation of species, we must take the view that transformation is an evolution of germ plasms. The hypothetical occurrence of a new species would thus have taken place in the germ-plasm of the parent creatures (*generatio spontanea in utero heterogenero* of older natural science). Following Rauber, we call it protogenesis. In this way occurred (hypothetically) the first chick; ever since chicks have descended from the fowl (deuterogenesis).

This view contrasts with the older one which considered that the germ-plasm of an organism was itself changeable during its life, so that qualities acquired by the organism appeared as inherited in the descendants.

If this theory of the inheritance of acquired characters were correct, then it should be possible in the sense of the exact theory of inheritance to prove that G was changed into G^1 by suitable changes in the external world. Important grounds have been advanced against this assumption. First of all, one consequence would be that it would be possible for organisms to acquire everything and to change the germ-plasm accordingly. Otherwise we should have to suppose limits placed to the power of acquisition—as in fact they are—and then we should get back to the germ-plasm as the starting point. It is in this fashion that experimental genetics to-day regard the case. Genetics recognizes no inheritance of acquired characters but only an inheritance of inheritable features.

The two most important objections to the possibility of the inheritance of acquired characters may be mentioned here. The first is concerned with the extremely complicated suppositions of this view (Roux). We should have to assume: (1) That the new character was introduced into the germ-plasm (translatio hereditaria); (2) that from its manifest (explicit) state it was translated, as it were, into the speech of the germ-plasm (implicit); (3) that it became firmly incorporated in the elements of the plasm (blastogenous insertion), which again demands various suppositions according as we imagine the plasm to be simple or already differentiated. In the first case, where the germ-plasm only gradually becomes differentiated, the "insertion" would act simply as a change in the primary stem gradually taking effect by a different course of ontogenesis. In the other case, where every particle of the germ corresponded to one or more peculiarities of the developed creature, where, therefore, every later manifest multiformity was already implicit in the germ ["Neo-evolution," para. 84], the insertion would have to proceed according to a quite definite type in order to introduce the changed or newly originated particle at that spot or into that combination where it could develop its characteristics later in such a way as to cause the characteristics of the parent-organisms to reappear.

Mention must be made of a second argument taken from the exact science of inheritance. This is a decisive argument against the theory of transference. We now know that a "characteristic" of the organism is often, perhaps always, dependent upon several factors in the germ-plasm, so that "it is only under their joint influence that a certain peculiarity (e.g., hair colour) develops." To suppose that conversely a newly developed characteristic might be so "inserted" into the germ-plasm as to reach the various decisive positions within the germ, is much more difficult than the explanation given above which satisfies all the relevant facts.

The employment of the theory of inheritance to explain causally the origin of organisms leads in actual practice to considerable difficulties, with the result that we have recourse to various hypotheses as to the particular circumstances under which historically G may have become G^1. Firstly, it must be assumed that the phylogenetic changes of G must have been much more extensive, and therefore much richer in result than they can be shown experimentally to be to-day. This assumption is justifiable because experimental genetics finds reasons for assuming that complicated phenotypic changes are traceable only to changes of some few factors within G. It is thus conceivable that, for instance, the cause of the whole mammal organization lay in comparatively few and simple chemical changes in the germ-plasm. Such "universal revolutions of the constitution" (Haecker) as would have to be assumed, would be quite capable of reconciliation with the above-mentioned hypothesis of regulated chance.

But even supposing science were to acquire greater certainty in this question, causal investigation of phylogenesis would still be faced by one special difficulty. The present presumption of all phylogenetic science is that the system expresses at the same time the genealogical reactions. It thus groups together genealogically according to external similarities, and divides according to differences. Whales and marine reptiles are allotted to quite different genealogical lines, and certain toothless mammals are placed together to form the order of edentates. In the main this is right, but it is not quite beyond all doubt. For since we are acquainted only with phenotypes and recognize the genotype only in phenotypic form, it is possible that different genotypes could give rise, owing to like external influences, to like phenotypes and like genotypes owing to different external influences to different phenotypes. But transformation applies only to genotypes. We should have therefore to base the genealogical relations upon such characteristics as are extensively independent of functional and external influences (organization-characteristics). To go further into this question here would take us too far.

(ii) Partial Selection and Personal Selection.

Para. 33. By partial selection is meant that process by which within the organisms the formation of the most enduring among similar elements is achieved, i.e., those elements which show themselves to be functionally most adaptable. Here we assume a form of competition among the parts of the organism. This idea of a "struggle of the parts" (Roux) in the organism may be only a mental picture, but it is certain that the bone cells, tendon cells, muscle cells, etc., react to functional stimuli in the most minute degree by the creation of an optimum of functionally adapted form. Partial selection is to-day the most important stimulus of all change of form and must be regarded as such in all historical development of form [para. 46]. As a result of this assumption we might imagine that the great decisive turning points in the historical growth of forms were actually "points" of time at which new forms of life arose, as it were, at one blow, not by slow processes of change by which individual organisms, e.g., man, were perfected. On this assumption the germ-plasm, distinguished by the possession of a hominide gene, was the starting point of living beings which under the influence of the external world at once developed into man.

Contrary to the common opinion that the assumption of the erect posture by an anthropoid ape gradually gave the body human characteristics, we imagine with Klaatsch that a definite organization must first have existed which made possible the assumption of the erect position. This applies particularly to the hand and foot, which as means of standing and gripping must have existed in the adaptable, specific rudiment if they were to be developed under the stimulus of function into human characteristics.

The practical use of the principle of functional adaptation is very great. In addition to the above-mentioned [para. 19] important rôle which it plays in regulation and reparation in the individual life, we may here allude to the change which undoubtedly takes place under the influence of environment. Acclimatization, the change of the form of the head of European Jews and their children in America (Boas), the origin of social types in a uniform population, all these belong here. The results of migrations may also be placed here if it is true that a rich geographical abundance of forms has arisen from a few simple initial forms under circumstances of progressive expansion and the influence of changing environment. We may neglect for the moment the fact that in some cases we have non-inheritable and in other inheritable changes. Functional adaptation would have to be taken into account of course, as R in our formula when considering historical transformation, although the truth of these "system-conditions" cannot be tested, for organisms, which have developed in the past, can only in very small measure be placed experimentally under different conditions. The question whether a character is an "adaptation character" and will change in a different environment is, therefore, for the most part unanswerable. And the division of the characters of an organism into "organization characters" and "adaptation characters" is hardly possible, and is better abandoned, since all characters considered as developed from the G of the germ-plasm are organization characters, and even transformations of non-inheritable kind, which are undoubtedly due to the influence of environment (e.g., a round-skulled race) could only arise from an area of the germ-plasm, capable of reacting to certain environmental conditions by a decrease in length of skull. It would be better to distinguish between architectural (constitutional) and functional (transitory) characters. The former would include those which arise under all circumstances (e.g., division of the visceral arches and ribs, number of bones of the skull, the segments of the extremities, the proportions, dental formula, lobes of the lung, etc.); the latter change with varying system-conditions (head, form, hair-colour? convolutions of the brain?).

If we interpret the formula to mean that with G^1 a new situation arises which becomes manifest by means of partial selection among already existing environmental conditions, then to understand historical transformation we must assume a preservation of this new possibility of reaction (i.e., of G^1). This assumption is satisfied by the third ætiological principle, that of Darwin's selection, i.e., personal selection.

(C) Transformation Theories.

Para. 34. This exposition shows that the older theories and hypotheses of the formation of species, however much they have furthered the advance of science, have only to a very limited extent any real ætiological value. If we are to recognize the cause of species formation in the change of G into G^1, neither Lamarckism nor Darwinism can be described as causal investigation, for in the formulæ $Pha = f(G. Ra)$ and $Ph^1a = f(G^1Ra)$ they either comprehend the first formula only which is not applicable to species formation, or they presuppose in the second the presence of a new G^1. Lamarck substitutes for the G the suitably reacting psyche of the animal and makes the new character thus developed inheritable. Darwin starts from the already newly formed G^1 and merely shows us how Nature behaves in order to obtain, to distribute and change further the $Ph^1{}_{abc\ \ldots\ n}$ and $Ph^2{}_{abc\ \ldots\ n}$ thus originated [para. 32].

In distinction from these the Weismann theory is based upon the true causal view that only a change of G can lead to species formation, although by the assumption of the inheritance of the germplasm through the inheritance of the persons possessing them he tried to make probable the development of smallest hereditary particles (determinants) into more perfect factors of inheritance. In this he comes into conflict with the more modern views of inheritance which do not recognize such determinants for every characteristic. The mutation theory of De Vries must similarly be included among the causal theories, although his supposition of changes in the germplasm through a series of leaps is not beyond doubt. Finally, we ought to include here the view of orthogenesis (Nageli, Eimer) and its continuation (Genepistasis, Jaekel), the character of which best corresponds with the probable phylogenetic processes. By orthogenesis we mean a progressive change in the germ-plasm, proceeding as growth does, leading to the continual formation of new forms.

If we endeavour to form a causal view of the course of the phylogenetic changes based upon what has already been said we must assume a progressive change in the germ-plasm, which must have been particularly intensive at certain times. It would need to consist of only comparatively small changes of the constitution formula (in the structural formula of chemical bodies, radicles, side-chains, many affinities) to have far-reaching influence on the form of the animal. Such a view justifies the question whether the basis is a new formation or the transformation of something that already exists. Quite contrary to the evidence, the older morphology (Plato, Geoffrey, Goethe) held the view that all variety arose only through the complexity already present, that something really new, arising as something not previously present, could not be entertained (Goethe).

For the phylogenesis it is apparent that the postulate of *G* and the necessity of equating all causal changes to changes in *G* compel us to attribute great significance to phylo-preformation. Apparent new formations in animals are clearly changes in what already exists to a much greater extent than the naive observer thinks; indeed, comparative anatomy forces us by the determination of homologies to refer everything to something else that already exists. It is, therefore, questionable whether we can point to any character that has arisen as something completely new without the intervention of something already existing. The science of heredity without being quite clear as to the fundamental significance of the question is in fact adopting a similar point of view when it seeks the origin of pairs of characters, the presence of which forms the basis of the application of the Mendelian rules. According to these rules the essence of hybridization consists in the fact that the sex cells of the two animals fuse, being distinguished by one or many pairs of characters of like kind. The effect is that one of the animals possesses a character which is absent in the other ($A \times a$, for example, A = black hair, a = without black hair).

As to the origin of pairs of characters, too, there are epigenetic and preformistic views. According to the one view (Bateson), the one character (really the factor on which it depends; we call it for the sake of brevity, the character) is new and is present in one racial representative while the other is actually wanting in the other parent (= null, nought, is absent). Or again, one may assume that both arise anew in the parents, but the absent is prevented from developing by the constitution of the germ and remains latent (De Vries). Both views are epigenetic and being based on phylogeny must be called phylogenetic. The theory of Plate goes very much deeper—(theory of the supplement of the fundamental factor). According to this theory the starting point of a new formation in the germ-plasm is the state in which a condition of tension due to certain constellations hindering the manifestation of a factor is present. If this germ-plasm develops we get as it were " no character ". This state of the germ-plasm corresponding to the absence of the character contains with regard to this character the " fundamental factor " ; but as soon as this state of the germ-plasm in racial representatives is changed as the result of metabolic processes, the factor is so to speak released and appears as the supplement of the fundamental factor.

This is a theory which follows thoroughly preformistic lines and one which permits us to refer the causal processes in the germ-plasm to internal changes within it, which we may interpret as an increasing development of complexity of form from an existing apparent indifference. On these lines phylogenesis is the visible expression of a progressive disappearance of hindrances in the germ-plasm.

The idea of orthogenesis best agrees with our present knowledge of phylogenetic change. It assumes a transformation of the germ-plasms resulting from internal causes and proceeding in a definite direction (Lubosch, 1924). Grosser (1926) has recently declared himself a convert to the theory of orthogenesis, which has always been strongly advocated by palæontologists. Bolk (1926) has recently given it clear and unmistakable expression. According to him evolution is not a result, but a principle ; it is to be conceived for organized nature as a whole and a unity, like growth for the individual, subject like this growth to the influence of external factors. These, however, can never create, they can only modify. Evolution is a function not of the individual but of the whole of life. What we recognize as evolution is the manifestation of the differentiation of the macrocosmic total organism (Bolk, p. 12).

(3) Relation of the Methods of Consideration to One Another.

The Interrelation of these Two Points of View.

Para. 35. We have already drawn attention in different places to the frequent close interconnection of the morphological and the ætiological ways of looking at organisms. It is now advisable once more to define briefly the limits and task of both. All forms are as such to be judged morphologically, but the form in space has an active and a dynamic quality. Furthermore, the form may change under the influence of stimuli, and above all it is the result of a developmental process subject to highly complicated conditions.

In view of our decided inclination to regard the causal manner of consideration as the specially scientific one it is advisable first to ask what are its limits. Now there is no doubt that we can only pursue a causal inquiry where we can establish changes. For this reason the changes of a form under the influence of environment and the ontogenetic changes that dominate the making of form will in particular be the subject of ætiological inquiry, and the question as to how the superficial limits of a form, its symmetry and polarity, come about may, if these be accepted as already accomplished, be approached ætiologically. We shall meet these questions and their treatment again when reviewing the tasks of experimental embryology. For the moment it will be enough to point out that in all these ætiological inquiries we are really dealing with problems of conditional investigation [para. 23, ff]. We have always to take into account the analysis of a vast complex of system-conditions which is given as a whole, viz., as the constitution of the germ-plasm. Thus the real cause remains as an unknown quantity in all investigations. Students of experimental embryology starting with an incomplete understanding of causes were surprised to find that experiments might have one result on the larva of triton and quite a different one on the larva of a frog. No wonder, for the real cause, the constitution of the germ-plasm cell, was different in the two cases.

With conditional investigations it is naturally the methods of the experiment which have to be taken into account. Only when the conditions are artificially varied is an insight into their normal interplay possible. Experiments on entire organisms (transplantation into another environment) and experiments on the germ-plasm differ in value. In the former we are able actually to determine the reaction range of a phenotype, and thus ultimately of the genotype. Such experiments as the tracing of the somatic changes under acclimatization, changes of head form, of body size under the influence of nutrition, serve to increase our knowledge of causality by teaching us within what limits the constitution of an individual living being lie. And the analytical experiments of experimental morphology may contribute to the same end if the outcome of identical experiments is tested on various ova. The differences, thus brought to light, are a good index to a judgment of constitutional differences.

The employment of these results has hitherto been much neglected; the initial conditions have been taken in the main as alike, and the examination of conditions has been confused with that of causes. It is an illuminating fact that, within an individual development, by means of analytical experiment, we may gain an insight into the nature of the conditions, but such an experiment, however, must disturb the cause which consists in all the natural conditions acting simultaneously.

Thus phenotypical experiments on entire organisms and analytical experiments on the germs of organisms are only of value at one remove for the investigation of causes. The investigation of heredity, on the other hand, possesses immediate causal value. This latter science is to-day divided into pure experimental analysis of crossing and bastardization on the one hand, and the study of cells on the other. Both these branches endeavour to determine by different means on what plan and under what forms the inheritable substance is contained and built up in the cell [para. 109]. The attempt to trace the effect of this substance in the appearance of the individual belongs here, too, so that genetics, the study of the cell and individual (constitution) anatomy in close connection serve to further our immediate knowledge of causation.

But we are not able to experiment on species of the animal kingdom, on families and the larger formal divisions. Man, too, exists as such, but all we can postulate [paras. 32, 33] as to his possible origin is a number of hypotheses possessing a certain measure of probability. The causes and conditions which have produced a bird, a mammal, an ape and our own race, can no longer be brought into existence.

We now know only the causes of their preservation (= absence of change of state in their germ-plasm). The causes of their production are gone; there is therefore no possibility of investigating their causes beyond quite definite limits. At this point morphology comes into its own; it therefore begins where the causal view-point fails us.

The relation of the two methods to one another thus depends on the exact extent to which they help us within the accessible living material, and therefore causally determined, to answer these two questions: (1) Under what phenomena, and following what rules do the given conditions in the germ-plasm act in order to produce a form embryologically? and (2) how do inheritable changes in the structure of the germ-plasm come about to such an extent that the transformation of one organism into another necessarily follows? We shall be able to use the results of these investigations, even if at first they are of small extent, to assume for that region which is inaccessible to the study of causation that things there too may be very similar. Sometimes, perhaps, the law of transformation may be enunciated with such clearness that we shall be able to comprehend the world of forms causally, at least as far as general causes go; that will probably be the limit to which we shall be able to go since the special causes, as has already been said, are no longer within our reach.

But this world of forms, and indeed all organisms, including man, has the right to be measured with a scale of its own which, in our condition of complete ignorance as to the causes of its origin, is offered by the archtectonic aspect. The astronomer deals with the regulated relations of the stars, their size and distance from the earth, brightness, their paths and their relations to one another.

He finds nothing but complete harmony; to describe them is his only problem; he is indeed justified in assuming some prime cause of the whole, but astronomy knows no science of causation. The relations between ætiology and morphology may be involved, but we can differentiate the special problems of morphology quite sharply, and can attack and pursue them accordingly.

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Special Section.

Special Morphology and Morphogenesis of Man.

Introduction.

(1) Problems and Methods. Observation and Memory.

Para. 36. Knowledge of the various devices by which the movements of the body are performed is acquired by a study of the preparations of the human cadaver and preparatory and accompanying instruction in anatomical lectures with the aid of anatomical text-books and atlases. We have already made the acquaintance of the difficult problems which the fundamental science of medicine places before us. With our first entry into the laboratory they face us in full force. This book is intended to form an introduction to these problems and to awaken the understanding of what may be learnt from the cadaver.

But it does not aim in any way at spoiling the first deep impressions made upon the unbiased beginner in anatomy at preoccupation with the objects in the museum. On the contrary, we desire to emphasize the value which impartial observation has for the study of of forms.

This book is intended to act as a spur to such study. The cadaver is, of course, not living man, and it has required, and still requires, much careful study to show in the living form what is shown by the cadaver. But all our knowledge of living forms would be incomplete and without stable foundation if it were not firmly based on the examination of the cadaver. This is true also of microscopic anatomy and the anatomy of tissue and cells. For the divisions of anatomy, too, must take dead objects for their study to which the examination of the living can only in small measure be added.

The material of the preparation room needs a special word of explanation. It is clear that the ideas which anatomists have formed for centuries past of the structures of the human body rest entirely on the nature of this material. The material is supplied by criminals, the diseased, and the old; in other words, by those whose lives have been overtaken by some unhappy fate. Children, young and healthy persons, those who have been successful in life, those who belong to the leading classes, are never or only by the rarest chance included. Anatomy, as collected in our textbooks, is thus pre-eminently the anatomy of a selection of material. The anatomy of these cadavers, of which we know no more, would under ruder conditions, no doubt, be the anatomy of Europeans in general as is shown particularly by pathological anatomical specimens. But we may justifiably assume that there are differences in many of the details which have escaped us.

Para. 37. Since anatomy is the study of the form of the human body, it follows that the comprehension of forms is the first and basic problem which has to be faced by the young doctor. " Form " in its narrower sense is, as we have already said, not only the form of the individual organs but also their mutual position (topography, syntopy i.e., the relative position, skeletopy, i.e., the position in relation to the skeleton), and finally, the form of the body as a whole.

For the study of the external form of the body the cadaver is but little suited. The changes produced by death and preservation of the body affect every organ and the whole body. None the less, the museum is an important department for the study of external form of the body and its organs, for the reason that we can recognize here how the whole form depends on the detail of the form of each organ, and conversely, how the external form lays down the plan into which the internal features are fitted. Thus we can study in the museum the significance for body structure of size and proportion of male and female, characteristics of youth and age, of coarse and fine, intense and lax constitution, and in this way sharpen our sight before turning to the living form. This sight is to a high degree an inborn gift, but it can and must be acquired by practice since it is indispensable to the doctor.

Let the study of form begin then as soon as the doctor-to-be sees his first cadaver. The study can only be actually followed by one method, that of observation immersing itself whole-heartedly in the object. The human body should be looked at as we look at a work of art, as a whole and at every stage of a progressive subdivision. Here for the first time we meet the contrast between observation and abstraction [para. 51] which for the study of anatomy is of such great significance. There is a similar contrast between traditional and acquired material for observation, between the atlas and the insight which we have gained for ourselves. The pictures in the atlas are of course the result of insight obtained by centuries of study and we must not despise the value of these aids, for no single man could determine anew the formal relations of the body without a vast expenditure of time and trouble. A lifetime of study would be too short. And so we have to make a compromise in the sense that we have to experiment independently and confirm our results by means of the books or, putting it the other way about, we have continually to verify what is in the books and atlases. Verification will often be impossible, particularly where we have variation from the norm [para. 41]. The textbook is an indispensable literary aid, while we may get on quite well without the atlas. In any case we ought at first, at least once, to attempt to comprehend the form of an object without assistance.

Next to the cadaver the best means for this is provided by the skeleton and the individual bones.

When examining a human humerus we should ask ourselves the following questions: How long is the bone (measurement)? How thick? Is it round throughout, or does it show some other form? (touch)? What portions of it impress us? What is their appearance? What conclusions may be drawn from the form of these portions as to the form of the neighbouring skeletal parts above and below (scapula, radius and ulna)? What is the nature of the surface (feel gently, touch with the more sensitive fingers, if righthanded touch with the left; touch with the finger tips, touch, not press)? Where is the surface smooth, where rough? What roughnesses are especially striking? Where are they situated (proximally, distally, on the medial or lateral side)? Which of them is the stronger? How does the axis of the head, the shaft, and the distal articular surface run? Are there depressions and foramina? It is a great mistake and one that will quickly avenge itself to suppose that the faithful study of the individual form may be neglected, or to despise the task of committing innumerable names to memory under the delusion that one may at once begin with something higher, like the functions, adaptation, relations to the whole, etc. [para. 15]. This supposed higher study is only the ripe fruit which can be gathered after long self-denying toil. Names are not only technical terms but also labels for conceptions. These have their roots in observations [para 5]. It is obvious that the names must derive their meaning from our observation of objects.

Thus the form only passess into the possession of our memory through the medium of observation; imagination is the reproduction of acquired observations from our memory. The other method, that of learning an anatomical form with the names from pictures, makes use of abstractions and thus leads only to the reproduction of abstract conceptions.

The great value of drawing (Bruns) for the acquisition of ideas of form, because drawing compels us to look, is well known. It may be confidently asserted that only one who can draw it, however poorly, has properly absorbed a form. At all events let the fact be taken to heart that we cannot really know either outline or detail in anatomy save by seeing with our eyes.

The would-be doctor has a long and weary road to travel before he can be acquainted with the forms of the body and its organs, their structure and the histology of the tissues and cells. And the way is made still more difficult by reason of the number of questions which entice the student into by-paths and divert his attention from the immediate goal. We do not desire in any way to detract from the value of these questions, but we have already pointed out that they can only be answered by one who has already mastered the forms. Among these questions the following should be mentioned :—

(1) The question of the origin of form (morphogenesis). This is of very great but secondary importance, since we must first know the appearance and the relations of a thing before we can study how it came about.

(2) The question of the purpose of forms. This has been discussed in para. 18. This question must always arise, because we face Nature as beings endowed with the power of judgment. But here too it must never be forgotten that only an exact knowledge of the given forms can give any value to the question of their purpose.

(3) The question of the function of the parts. This is an unavoidable question, but here the same thing is true. Only exact knowledge of form justifies our asking what is its relation to some function. However attractive it may be to attribute the origin of a form to some function, and however unusual this treatment of anatomy may be, we must remember that, as has already been said, form has it own laws [para 26].

(2) Anatomy as the Subject of Plastic Art.

Para. 38. At this point we cannot refrain from reminding the reader that human anatomy is of great importance for art too. Plastic anatomy is not merely an anatomy of the external body form. For one who looks at the external form of the body without knowledge of the interior will undoubtedly fall into errors (Goethe), and in his attempts to imitate it will be like a man copying an unknown writing. Here, too, the fundamentals are the skeleton and the articulations. The situation and the grouping of the muscles and their contractions with the various positions of the body must be well known if a work of art is to be created in close imitation of nature. The skin is, so to speak, transparent, and allows what is within to appear on the surface. The surfaces of the muscles, their extent, the uncontracted sinewy components, the blood-vessels, the bony points give the relief. The amount of fat regulates the prominence of these, and differentiates male from female. The organs within the thorax and the abdomen are of importance in moulding these parts. The proportions of the body must be known, and above all the means by which the soul finds expression in the body. This means not only the facial expression, but also the carriage of the whole body, breathing, muscular tension, movement, even the outline alone (silhouettes) can convey a definite expression, since the outline is necessarily the total result of the position at any moment of the whole body. Thus a knowledge of anatomy is indispensable to the creative artist. But it also increases the enjoyment of those who only look at works of art. We do not truly see a thing until we know it, and in knowledge is the completion of observation (Goethe).

At this point two questions arise which we must not overlook. The first is that of the freedom of the artist in copying the object, and second, that of the objective criterion of the beauty of the human form. With regard to the first of these questions it is worth noticing, in spite of what has just been said, a plastic work of art is something more than mere objective reproduction of the model. It is not the object, but the work of art which forms the subject matter of art. But this follows definite æsthetic laws, which stand side by side with and are superior to the laws of anatomical correctness (cf. for what follows, Hildebrandt). The work of art is created as an appearance of reality, while the model presents itself to the observer in changing positions, and thus makes it possible for him to comprehend it in three dimensions. The work of art is confined to a single position and produces its effect upon the imagination of the beholder through the eye, and he imparts life to it by a psychic process.

The human form in painting and sculpture is in the first instance only a surface picture; the idea of depth must be forced on the observer by the technique of the artist. The representation must appear clearly in all its parts, while in Nature we see clearly only that upon which we direct the sharpest vision of the retina, so that we only see a complete body when it is at a great distance. Thus we have the paradox that we have to see a "distant picture" close at hand (Hildebrandt). What the artist depicts then, is not the object but the ideas of the object; what the observer sees is an idea of the artist, which under the influence of the artist's technique he converts once more into an object. The physiological and psychological optical processes in the artist's mind thus transform the object. It is erroneous to suppose that the given proportions of a body ("picture of existence") must be present in the picture made by the work of art ("effective picture"), and that the same proportion must reappear when the same object is placed in a different position or depicted in a different situation. In spite of the identity of the person such changes in space are not accompanied by identity of effect. To obtain a correct effect, what is objectively wrong may therefore be and often is depicted. The curves of a thorax may have to be emphasized for the sake of contrast if it appears too flat in consequence of powerful muscles in the shoulder and arm. Much that appears idealized or conventionalized may be there because it is necessary to the effect.

The work of art represents a body inspired by a will, and the effect of the work of art on the beholder rests upon the success with which the expression of a certain character in a certain situation is portrayed. These facts are of great influence upon the relation between model and copy. In this way the work of art becomes the embodiment of an idea, the expression of an inner truth [para. 1]. The contemplation of a work of art such as Klinger's Beethoven will perhaps best enable us to understand what is meant by this. A feeling of spiritual greatness, of the dominance of a powerful will over the body, is here forced upon the beholder by the sight of a majestic head with a high forehead set upon a weakly and, in many anatomical features, even a phthisical body, while, at the same time, every superfluous muscular movement is avoided. Thus the will, unhindered by muscular exertion, can exercise a purely mental influence visible even in the clenching of the fingers. We may contrast with this Michael Angelo's fettered slave, where we have the spectacle of complete impotence expressed not only in the suffering expression of the face, but also in the looseness of the limbs. We are led ultimately to demand that the body dominated by the will should be made the expression of each and every mental performance. Zeus, enjoining silence by the movement of his eyebrows and the shaking of his locks, so that the very mountains tremble, illustrates this in every feature of his head. The visionary musician (Liszt's statue in Weimar Park) shows it in his—for this very reason—unnaturally lengthened fingers. Anatomical "correctness" thus submits to the higher law of æsthetic truth [para. 1], which rules according to the idea entertained of the individual being depicted. Expressionism relies on this law by ultimately reaching the position in which, for instance, the idea of long is embodied in unnaturally lengthened bodies; it is able to take refuge in the principle that what is anatomically correct is not the supreme law of the artist. The dangers are obvious, since the boundary between caprice and inability on the one hand, and the newly created expression of what, æsthetically, is universally felt to be subject to law on the other, is a very fluid one.

But this glance at the limits, which are set to correct anatomical drawing, exhausts only a part of our question. There is still the second question, whether we can find an objective criterion of beauty in anatomical contemplation of objects alone.

E. Brücke has attempted in a fundamental work to elucidate the beauty of the human form objectively. The young medical student will find here (cf. also further literature) abundant instruction on the question of anatomy of the living and its value for art. Brücke calls beautiful "that form which may be used with advantage in any position and when viewed from any angle."

The attempt to sharpen in this way the appreciation of the beholder of what is harmonious and pleasing in the living body, and to demonstrate how creative art has made use of it, is completely justified. But the fact is often overlooked, that Brücke deals only with the beauty of the model and not with that of the work of art, and that he himself points out in various places how interpretations of this beauty differ, and how frequently lack of beauty in the model may be found associated with æsthetic beauty (Rubens, Botticelli).

Taste and our ideal of beauty change; at various times man has had various standards of beauty; there are few masterpieces the beauty of which is always apparent to us. Philosophers tell us that beauty cannot be objective, that it is not a quality of things themselves, but only of our judgment of them. The beauty of a work of art is thus placed on a like footing, with suitability to purpose in nature. Beauty is a state of the subject, because the feeling is the condition under which we conceive it. Beauty is form, because we behold it, but it is also life because we feel it. In a word, beauty is at one and the same time our state and our act (Schiller, *loc. cit.*, p. 89). This idea of beauty is at the same time not merely the result of experience; the germ of beauty is in each one of us, but in the artist it has reached its full development. Pleasure and its opposite in the impartial beholder, and the universality of these feelings, are the characteristics of that ability to judge which leads to the verdict of beautiful or not beautiful. The source of the ability is the feeling for the degree of agreement of an object with the idea of man, not merely as a representative of a species, but also as a moral being. Accordingly, that work of art is beautiful which most purely depicts the human body with the characteristics of the species, and which by its depiction puts us into that state in which we perceive this agreement. Every man, but in a much higher degree the artist, compares the objects of his environment with an ideal of this kind. Once certain anatomical relationships and proportions, and the manner of giving anatomical form to the spiritual in a certain way, have been acquired as the objective embodiment of the beautiful, they can become traditional and thus give rise to the belief that beauty has objective existence (Bulle).

The deep influence upon us of Greek plastic art in particular appears to rest on the fact that here objective beauty in the depiction of the human body is actually achieved, so that we are apt to regard Greek statues as the canon of beauty for all time. So far as this is true (see below) it is not due to any preponderance of beautiful men and women among the Greeks as compared with ourselves—although the Greek morality made ugliness more difficult in the life of the people than has since been the case—but rather to the fact that the Greek artists, when plastic art was at its zenith, were more harmonious men (Schiller) and had more immediately before them the connection of the sublime, bold, lovely, inspired and pious, with the total expression of the body, than was the case with later modern artists who, like all post-Greek humanity, conform less to one mould of thought and feeling. It is to this unity of the whole man, to Greek humanism, to something subjective, therefore, that we attribute the beauty of Greek art. It is for this reason that their representations of the gods are splendid men, while races equally well-formed physically have created images which fill us with horror. It was not by selecting the finest parts which he saw around him, and forming them into a whole, that the Greek master first made a beautiful human being, but by understanding how to recognize the ideal in the incomparable choice which his environment placed before his eyes. Just as Plato had recognized, in the thousand of individual things of beauty, the ideal beauty broken into a thousand fragments, the Greek artist saw this idea of the beautiful separated into innumerable individual phenomena. He created his work like the original model. In this way he could even achieve forms which were never realized in actuality, and which yet seem to us the noblest embodiment of pure humanity. The forms of the Greek gods and heroes are " prime forms " in Goethe's sense of the words. As an example, we may think of the horses' heads in the Parthenon; they depict a horse such as never lived anywhere, and yet with all the beauty of every possible horse, a true horse of the gods (Goethe xii, 147).

That which is anatomically incorrect is placed by all this in a new light. We are familiar with a number of such peculiarities which must be described as incorrect, e.g., five divisions of the abdominal wall, the relation of the width of the face at the level of the eyes to the height of the face, the exaggerated steepness of the profile, the forehead and nose, the longer second toe. The last is not absolutely incorrect, but is not usual, though it occurs on the Mediterranean coast. The other characteristics only occur anthropologically in a degree approximating to that depicted by the Greeks; the indices of those features in the ancient sculptures fall far outside all racial standards (Gaupp, Braus). It is noticeable that the degree of difference from the norm is used as an art fashion defining periods and schools. That they should become a fashion after their effect had been proved is intelligible, but why did the artists gain their effects by these means? We have already suggested their possible significance for the impression of the "effective pictures." It may also be the case that they were the means of expression which served for the attainment of the total impression, much as, for example, the impression of the heroic and divine is obtained by the increase of Aryan orthognathism, or as the impression of superhuman strength in the ventral muscles is increased by exaggerating the soft parts of the pelvis. For all these points, the facial form, the proportions of the toes, the length of the leg, the unusual lateral displacement of the ankle-joint, which, as far as I am aware, have never been mentioned, but which are particularly striking, we are without means of judging.

Carried to the utmost extreme such rejection of what is anatomically correct leads to geometrical conventionalization. It is always a sign of the more mature art of expression, while the pure art of impression stood at the beginning of the development of art representing the imitation of that which exists with entire freedom from reflection on the artistic effect. To this type belong the oldest artistic monuments of the human race, the coloured cave pictures of Palæolithic man in the caves of Northern Spain and Southern France (cf. Kallius).

In later, and particularly in modern art the contrast between the objectively true and the ideally beautiful is often much greater than it was among the Greeks, for the increased and much more complicated psychic life sought other means of expression. The essence of the æsthetically beautiful is therefore here much more difficult to seize. It is just for this reason that we turn again to the art of the Greeks, although there is no doubt that this contrast already existed with them too. Greek art shows us, however, that æsthetic beauty depends not upon objective truth, which is always relative, but upon ideal truth, which, being an ideal, is always single. As poetry depicts what never has been and yet never grows old, so does the artistically beautiful depict the formally true which is embodied in objective phenomena only in an approximation [para. 1].

It is on this that the high educative value to the anatomist of studying works of plastic art is based. If he descends from the sphere of the impartial æsthetic enjoyment to that of proof of the anatomy of a work of art he will reap a great reward when he recognizes how the whole, the expression, the inner life, dominates the anatomy of each part, and how, not only what is objectively correct but also what is not, contributes to a tòtal effect of irresistible truth.

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(3) Gradation of Objects for Anatomical Study.

Para. 39. When we have recognized that it is the province of anatomy to study the form of the body and its organs, that its subject matter is the form of man, we have made a considerable step forward. But this fundamental, apparently so simple, statement contains the germ of great and really insoluble difficulties. They lie in the word "man." The study of the human body can only be pursued by using individuals [para. 41].

Every cadaver is an individual type, and therefore has peculiar features which do not recur. Closer comparison would reveal that every organ in microscopical structure, even every element of the organ, possessed its individual character. Then there is the further fact that the structure of the body is not studied in individuals of the same age and sex. Hence in points of detail we have a mass of differences in the museum specimens which confuse the beginner, and lead him to ask why it is that the results of his examination of the museum material do not agree with the descriptions of the textbook (Lubosch). To attempt to describe the individual anatomies of every possible individual would naturally be as impossible as it would be ridiculous, for in spite of pronounced individual characteristics, human beings show so large a measure of agreement that the adoption of this agreement as the basis of description (i.e., the description of a norm) is a necessary simplification (normal anatomy). Both the individual and normal anatomy will be treated systematically later [para. 41]. At this point we shall only remind the reader briefly of their relation to one another, which cannot be made too clear to the beginner.

The norm is necessary, since it alone is accessible to the formation of concepts, and is thus the sole vehicle for our ideas of objects; just as without concepts in isolated ideas there can be no thought, so there can be no science without abstraction from the individual. Anatomy as a science is thus only possible if we dispense with the individual; none the less, everything individual is included in the norm, which, therefore, in the textbook has an element of approximation (e.g., the number of renal pyramids 10 to 14). Anything falling outside the normal is described as a variation, and there is considerable elasticity in both terms "normal" and "variation." The difficulty lies in the fact that to the doctor the individual exists as an object, but not the "norm" of man, and further, that all causal processes, are in the long run only given for one, and are therefore individual systems. Prophylaxis, therapy, and prognosis, all medical treatment and thought, all come together in a point of judgment of the individual. This is why, in the medical system of to-day, what is constitutional has come to be of such great significance, while anatomy by its whole nature must neglect this aspect, and put the norm in the foreground. From this dilemma there is only one way out, to develop individual anatomy, too, as a science, with the object of enabling more accurate conclusions as to the individual form of the norm based on external observation of man within the limits set to medical investigation. At present a beginning has scarcely been made in this direction. The medical student must therefore all the more regard it as his task to interpret without prejudice every individual relationship presented to him in the cadaver and museum preparations; indeed, he will be wise actually to seek diligently for individual variations from the descriptions in his textbook and atlas. The external body form, the movement and behaviour of our fellow-men, are aids to practising our observation of the individual.

But the normal as the object of "normal anatomy" also has its definite limits. For only groups of men as like one another as possible give a uniform norm. The greatest similarity to one another is possessed by men of like descent; for this reason members of the same family or race form groups. Normal anatomy, as it is taught among us to-day, is thus the average anatomy of the European races. But this race is not uniform, but is divisible into numerous subraces, which by intermixture have given rise to extremely complicated groups of forms (populations) [paras. 28, 45]. The European populations are mixed groups of this kind in which all or some European racial components are represented in various degrees. As a result of this the norms for the separate populations differ, and the preparation rooms of German and non-German Universities will differ from one another in the norms they show. Varieties and individual differences, frequent at one place, will be rare or non-existent at another.

The investigation of these questions is still in its early stages; light is thrown on the extent of the divergences by the fact that in Switzerland the tenth rib is a "free" rib in 75 per cent. of cases, while in North Germany, as a rule, the arch of the ribs is closed. On this point then the anatomist who travels from north to south must learn afresh (Frey).

Unless we pass beyond the limits of the European races our anatomy becomes too narrow, for the norms for the yellow and black races differ from ours. And therefore the divergences from the norm in the yellow and black races are numerically quite different from ours. What is a variety with us may be normal there. Particularly is this so in the muscular system (quotations in Fischer). With regard to vessels, nerves and inner organs, unfortunately little is known in this respect at present. If we want to get a norm valid for all human beings, we must go further and take the species as the basis of description. And this is in fact the theme of our anatomical textbooks. In contrast to the given object this is, like all systematic description [para. 28], colourless and, in spite of all definiteness in the conceptual, it can in no case completely comprise the given object.

On the other hand, taking the species offers a certain advantage, for while it emphasizes the contrast between individual and normal anatomy, it eliminates it too. For while normal anatomy takes the species *Homo* for its theme, excluding all that is peculiar to individual and race from its presentation, and making racial and individual anatomy a special province, it also throws a bridge between human anatomy and the anatomy of mammals and vertebrates in general. Human anatomy can now be treated as that of a member of a higher category. If the fluid picture of the individual grows ever more immobile under conceptual treatment, yet the rigid features are animated when we recognize in them the characteristics of species, order and class, and when a certain formal character presents itself dominating vertebrate organization, or even the whole animal organization in general. For the causal interpretation of organizations individual anatomy performs a great service, for the morphological formal interpretation it is at first of less importance than "normal" anatomy. But without it any comparative anatomical evaluation of the human organizations is impossible. Thus as soon as we enter the museum our two great principles of interpretation face us at once in the same cadaver, presenting to us the riddle how, where, and according to what principles the "normal" and the "individual" are united in the single being [para. 109].

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(4) Division of the Material.

Para 40. Anatomy as morphology requires supplementing in two directions: we want to learn the origin of the human form and to gain an insight into its inner structure. The former is the province of embryology, the latter of microscopic anatomy. As these provinces of anatomical science are taught, their inner connection with anatomy is beyond all doubt; the one presents the gradual growth of the final state, the other a long series of single pictures of the finer structure of the organs after the cells and the formation of tissue from the cells has been described and demonstrated by means of preparations. But the same question faces us in embryology as in the developed form: What is its universal law? It is not enough [para. 72] to know the single phases of man's development; we must also learn if the development of man has followed this course and no other. It is by comparison that we grasp the necessity inherent in this wonderful process, and it is comparison which shows us how the type of vertebrate ontogenesis dominates human ontogenesis, although so altered is to be almost unrecognizable. Ontogenesis becomes morphogenesis.

With regard to the structure of the organs things are the same. Here it is at bottom all one whether we examine the finer structure of a human or an animal organ, since the tissues of which the organs are composed are always the same. The difference is in the specific development of the individual components. What is typical in the structure of the cerebral cortex could, for example, be better illustrated in the brain of the mouse ; what is typical in the mucous membrane of the stomach could be more easily demonstrated in the cat than in the human organs. It must be shown in the latter, however, because the physiology and pathology of man, which come later, assume a knowledge of the structure of the human organs. Thus, morphological problems, important as they are, are thrust in the microscopical anatomy of the organs more into the background. But they have all the greater importance for histology, for here we have something common to the tissue structure, not only of all vertebrates, but of all animals, and this common feature must be extracted from the multiplicity of individual phenomena and placed in the clear light of knowledge. The final step leads from this histomorphology to cytomorphology, for obedience to laws in tissue formation depends upon obedience to laws in the structure and life of the cell which is to be examined last. No limit can be reached, for what is visible in the cell is only a phenomenon of what is invisible ; the stream of the morphology of man flows into histology, the morphology of molecular compounds, molecules and atoms (leptonomorphology, leptos = fine).

And so the way is pointed towards our further exposition. We must turn first to the principles of morphology, then to those of human morphogenesis, and finally to those of histo-, cyto-, and leptonomorphology. Within the first and more comprehensive section we shall begin with individual and average anatomy, then comes the consideration of anatomy from the standpoint of racial anatomy, and this will be followed by human anatomy from the standpoint of comparative anatomy.

(I) Special Morphology of Man.

(A) Morphology of Man as an Individual. Individual and Constitutional Anatomy. Questions of the Norm.

Para 41. We have dealt with the nature of individuality already; now come two questions: What anatomical phenomena does the individual present? and, What is the origin of the individual?

With regard to the first question, it must be remembered that individuality has not only an anatomical expression, but that the ultimate reason for this anatomical individuality is found to be a chemical individuality. For every individual bears with it from the fertilized egg the individual plasm, which passes over into all its body cells and their products (intercellular substances, tissue fluid, blood-lymph, secretions, excretions). This individual plasm is molecularly and "supramolecularly" (structurally) specific (Grosser). As something specific for the species this individuality has long been familiar (Rabl. Huppert). Our attention was first directed to it by failures in transplantation, and these have been confirmed by the results of serological blood-reaction. Improvement upon these methods and the result of transplantations has, however, taught us that the chemical "peculiarity" must persist in further gradation right down to the individual. Only when an organ is transplanted from one part of the body to another in the same individual (auto-transplantation) is it really so preserved as to become a part of the organism. All attempts to transplant an organ from another individual of the same species for curative purposes have failed (Borst and Enderlen). The biochemical differences in the tissues of the two individuals lead to the destruction of the implanted organ, which here plays the part of a scaffolding into which the tissues derived from the host grow. With early embryonal transplantations the case is otherwise. Not only do parts of different species fuse in this case (Spemann and Mangold), but even, for instance, the tissues of frog and triton (*idem*), i.e., of two different orders. We cannot at present say how these tissues would agree with one another in fully-grown bodies, since the growth products have not attained long individual lives.

Anatomically the nature of individuality is revealed first of all in the micro-proportions of the tissue cells. Syntony and harmony [para. 105] are obviously those conditions of histological structure on which the firm connections between total size of the body and size of the organs (perhaps form of the organs too) are based. To this extent they are also of importance for our interpretation of many individual features, which are connected with the factor of total size [see para. 25, p. 78].

The less fine characteristics of the body may be expected to differ more strikingly in proportion as the individuals are less nearly related by blood. Twins from a single ovum should be most like one another, and it is a fact that there is generally a very large number of like individual characteristics present in these cases. But in spite of this we cannot speak of identity.

In particular such features have been tested (Poll, Wilder, Ludwig) as belong to the finest expressions of individuality (the hair, whorls of the finger-tips and in the palm of the hand), and it has been found that characteristics which are of extremely rare occurrence are found in both twins (imparted to both from the same individual plasm of the egg-cell), but that distinct divergences also exist. The possibility of confusion of the two twins was always ruled out on close examination. These investigations, which have also been carried out with like results on armadillos, reveal to us the most minute differences in the individual with which we are acquainted. They show that identity of two individuals does not exist and cannot be expected.

It is not the province of a science to mention or describe all the variations which exist between two individuals. But, on the other hand, it may be regarded as its function to determine the directions in which individuality becomes apparent and to seek the rules governing the formation of individual entities from isolated characteristics.

It has already been stated [paras. 25-27] that all anatomical characteristics fall from the standpoint of appearance into three groups: Quantitative, formal and topographical. Of these, the last two may be termed qualitative, in contrast to the quantitative characteristics. In all three groups individual variations occur.

Quantitative are all those characteristics which can be immediately expressed in terms of number, measurement or weight (size of the whole body and its parts; the proportions of the parts to one another, absolute and relative weight of the organs, i.e., weights related to body weight, body size and other standards of comparison; absolute and relative length of the intestines). The most important quantitative characteristics are those which exist in organs of frequent occurrence (meristic characteristics). Vertebral columns, ribs, bones of the hand and foot, number of spinal nerves, play a conspicuous part here among the larger elements; of more minute features we may mention the number of circumvallate papillæ of the tongue, the number of nerve-endings in the skin, the number of hairs in any surface area, the number of gland lobes, lung lobes, renal pyramids, calices of renal pelvis; and, among the most minute, the number of the nervous elements of the retina and their reciprocal relations in the retinal layers, the number of taste buds, the number of the ganglion cells of a nerve nucleus, the number of fibres of a nerve and many others.

In all these cases normal anatomy is content to give limiting values which satisfy the needs of the anatomist, but not those of the doctor, for the number of the distinctive elements is of obvious significance when a judgment has to be formed of the individual keenness of sense organs or of the capabilities and resistance of a given kidney or digestive apparatus.

With regard to the forms of organs, the appearance they present displays the greatest variation even to the outward view. Body form, nose, ears, mouth and eyes differ individually to such an extent that identification is possible on any one of them, provided that it is systematic in every detail (e.g., Bertillon system, basing a man's identity in criminal investigations upon eleven characteristics of the body; see Martin). Research has shown that the physiognomical impression made by a part of the body, e.g., the nose, must be attributed to numerous separate characteristics, each of which is like a tiny stone in a mosaic, obeys its own laws of form and inheritance. The shape of the nose, for example, depends upon the skeleton, the shape of the cartilage, the thickness of the soft parts, their development, and the play of the muscles. The bridge and tip of the nose, its length and breadth, the position of the nostrils, are, in their form, independently inheritable and inherited characteristics (Martin). In the hand and foot, one notes the proportions, breadth, length, slimness or plumpness, curve, flatness, relief of muscles and tendons, skin markings, amount of fat. For the internal organs exact determinations of form are for the most part not yet established. Best known are the variations in the brain, lungs, stomach and liver, but even in these cases the facts with regard to all the varying components are mostly unknown, or at all events, by far not so well known as in the nose, ear, eye and mouth. And in all this we have in mind only individuals of the same age and sex; if we extend our examination to differences of age and sex, the individuality of formal characteristics is enormously increased. At present we possess no anatomy of age at all, with the exception of certain attempts at the anatomy of young children.

Even more neglected at present is the question of variation of position, the importance of which for individual anatomy is very great. The position of the organs in the body is in its outlines one of the most constant conditions of an organism; the homology of the parts is based upon it [para. 27]. In the main, individual variations in the positions (on a large scale) of the parts are rare for the reason that they can be traced back to definite topographical relationships of the primitive organs. It would appear that those organs are most subject to individual variation of position which only attain their "normal" position at a late stage in development, while topography is stricter in proportion as it is reached earlier in ontogenesis, i.e., the older it is phylogenetically. The smallest variations of position are accordingly shown by the skeleton, muscular and nervous systems (displacements of the vertebræ), combined with changes of form at the limits of individual zones, e.g., assimilation of the atlas to the occiput, cervical ribs, or the absence of first rib, 13 or 11 thoracic vertebræ, 4 or 6 lumbar vertebræ, 6 or 4 caudal vertebræ, displacement in the segmental relations of the nerve plexuses. Variations of position in the vascular system are more frequent and commoner in the veins than in the arteries. In the arteries the phylogenetically older position is often restored (variants in the origin of the aortic arch, in the course and position of the arteries of the arm [A. brachialis anterior]; of the branches of A. hypogastrica [A. obturatoria from the A. epigastrica; A. ischiadica as end branch of A. glutæa inf.]; of the arteries of the thigh: abnormal origin of the A. circumflexa femoris; of the arteries of the lower leg and foot: A. dorsalis pedis from A. peronea). In the veins the frequent persistence of a left vena cava superior is important. Next in degree of frequency come variations of position of those organs which only attain their final position after much movement and displacement (kidneys, gonads, cæcum). The most frequent variations from the normal position are shown by the large intestine in its ascending and transverse portion, while of the descending part only the sigmoid flexure varies much in its position as a rule. This is explained by the developmental history of these parts. The thoracic organs are most constant in their position, although here, too, no doubt as the result of the late perfection of the form of the human thorax, many interesting variations of position occur. The most familiar is the variation in the course of the limits of the pleura (Bluntschli). Finally the morphological appearance of individuality is influenced to a high degree by the fact that the time factor of development is dominated by the constitution. Ossification provides an important example of this. More pronounced ossification (e.g., the cartilage of the ribs, of the sternum, of the larynx) by no means runs parallel with increase in age (Lubosch). In small individuals ossification of the epiphyses is retarded, in large ones it is accelerated (Hasselwander).

These hints may perhaps suffice to sharpen the student's sight for the development of individual characteristics in the objects which he studies. For greater details he must be referred to the literature quoted. Attention to all the variations which are met with represents an important step in the study of individual anatomy. Of greater significance is the question according to what rules the single characteristics combine to form an individual total organism. This is effected first by the combination and then by the correlation of the characteristics. By combination we mean that characteristics come together by chance and subject to the laws of probability; correlation is the non-accidental common occurrence of two or more characteristics such occurrence being due to common origin.

Para. 42. With regard to combination of characteristics we must first remind the reader of what has been said in the sections dealing with causality as to the connection between obedience to statistical laws and the development of form. A certain measure of insight into individual combinations of characteristics may be gained by means of the following remarks.

The comparison of numerous individuals as to one single characteristic enables us to plot the curve of probability of this characteristic. In homogeneous material this curve encloses an area containing a medial distinct field. This is bounded by two ordinates between which half of all the observed variations of the characteristic lie. The two ordinates are distant from the "mid-value" on the + and — side respectively by the "probable variation." The remaining half of the observed variants lies to the right and left outside these ordinates. If we compare 1,000 men, for instance, as to the number of their thoracic vertebræ we shall get a certain number of men far outside the probable variations (those having perhaps 10 or 14 thoracic vertebræ). If the comparison be extended to several characteristics, e.g., abnormal course of Ar. obturatoria, presence of an excessive number of bones in hand and foot, foramen ovale in the heart, abnormal lung lobes, then for each separate characteristic a greater number of men will again be outside the probable variations. But those men who are far outside these limits in all the characteristics at once become less and less frequent, in proportion as the number of characteristics increases. A man who comes far outside these limits in the number of vertebræ, for instance, loses this special position when a combination of twenty characteristics is taken and becomes more and more "normal." An increase in the number of the characteristics thus narrows the area of variation of the probable variants to the mid-value. And while the so-called "average man" is a fictitious being who is supposed to possess the mid-values for all characteristics, the "individual" man is a creature whose separate characteristics, though they do not coincide with the mid-values, yet lie within very narrow limits on each side. Imagine a curve drawn for a single characteristic in a large number of men and then imagine the curve of all characteristics in a single man in which every characteristic has its place defined by ordinates and abscissæ. This total curve for all the characteristics of an individual and the curve for one characteristic of all individuals would show approximately like form (Heinke). If the degrees of development of the single characteristics occurring within the probable limits be taken as units, then it may be said that individuality is a permutation of these units. This may be made clear by an example (Heinke). Suppose each characteristic to be an urn in which a limited number of balls representing variations of this characteristic is placed. "We get the first individual when we arrange the urns in a row and take out a ball from each urn in turn without looking." In nature this extraction and combination of the balls in our example is performed according to a widely held view by the reduction-divisions of the sex cells and the amphimixis in fertilization [para. 109]. It is evident that this forges a link with our interpretation of the concepts of type and metamorphosis; for the type is the sum of all probable [not of all possible, para. 24] characterization, while metamorphosis represents the actual permutation in a single case. If it were possible with a homogeneous collection of human beings to determine the sum of all probable variations of a single characteristic (which is not possible), and if the number of individuals were defined (which it is not), then we could in fact calculate all possible individuals. "Each would be equally probable, equally most probable and each equally normal" (Heinke).

This exposition gives at the same time an insight into the nature of variability which by many is still looked upon as a process. It is only a process if we go back to the source of the new formation of forms [germ-plasm mutations, para. 32]. This is certainly a process which creates a quite fresh system of permutation (new unities which are mutated). Within such a system, however, i.e., in the case of all groups of forms now existing, variability is a state. Variability, further, is not unlimited and not free from laws, but is the definite result of permutations of characteristics under unchanged conditions of life. The view that pronounced variability only occurs in domesticated creatures (including man) is also a false one. On the contrary it has been shown that variability in wild creatures is like that in man (the herring, Heinke; the orang-utang, Selenka). In the herring racial formation has been demonstrated in just as pronounced a degree as in man in the shape of the head, the number of scales, the position of the fins and various other characteristics. That this must be so is apparent from what has been said above.

Para. 43. In contrast to combination, the correlation of characteristics represents a relation of characteristics to one another. This relation is of such a nature that changes of one characteristic are connected with those of the other characteristics in accordance with certain laws. The measure of correlation is the coefficient of correlation $\pm r$, which is a positive or negative magnitude between 0 and 1.

If $r = 1$ the correlation is complete and the changes are identical; if $r = 0$, there is no correlation at all. A positive sign means that the characteristics grow or decay in like fashion; a negative sign indicates the reverse. The correlation of two characteristics has also been shown by a graph. (On this and the preceding, see Martin, p. 78.)

It is a simple matter to define the correlation, if characteristics are compared which can be grouped at once according to class-variants, or, in other words, if the characteristics can be interpreted numerically; if, for example, it is asked whether within a population having a certain body size a definite proportion of the thorax, width of the sternum, length of the thigh are correlatively related. The question becomes difficult when it involves characteristics of form and situation which can only be defined according to the frequency of their occurrence, i.e., characteristics which can only be classified by some artificial means. Dunker's correlation formula states that the frequency with which various characteristics occur together in an individual can be calculated from the product of the number of cases (n) divided by the (n-1)th power of all individuals. Let us suppose that in 1,000 cadavers an abnormal A. obturatoria is present 450 times, that 6 lumbar vertebræ occur 180 times and a processus supracondyloideus humeri once, then the number of men in whom all three characteristics would occur together would be $\frac{450.\,180^2.1}{1000} = 0.008$, i.e., only one man in 125,000 would have all three characteristics. The details of the difficult calculations need not be gone into here (cf. Martin); our object is rather to show the significant aspects of the whole question (for correlations based on calculations of greatest frequency values (see pp. 151-152).

It is a well-known fact that "correlated variability" plays a great part in comparative anatomy and in the question of formation of species (Darwin, "Origin of Species," chap. i). As examples we may cite deafness in cats of white colour with blue eyes, immunity from poison in black animals, greater sensitivity to disease (tuberculosis) in albino animals and humans, defect of ectodermal primordia of organs combined with leucism [mammary glands, caries of the teeth, short sight (Paulsen)]; more pronounced susceptibility to alcohol in white mice (Stieve).

Modern clinical study has tended increasingly to recognize that susceptibility to certain diseases goes along with certain bodily characteristics. Characteristics which are indicative of such susceptibility to disease are termed "stigmata." These may differ widely in nature, e.g., obstructive formations, infantilisms, theromorphias, progressive variations, etc. The sum of all characteristics in correlation or combination makes up the constitution of an individual. And the susceptibility to certain diseases which has its basis in such a constitution must be regarded as a correlative union of certain characteristics with other characteristics.

It is in this, with the present state of uncertainty regarding stigmata, that the fundamental importance of individual anatomy as a science lies. The question with the answer to which we are here concerned is then as follows: If a germ-plasm constitution exists which is genotypically so changed that from it an individual originates disposed in some direction or other to the appearance of morbid changes, are there then anatomical characteristics standing in constant correlation to this state of the germ plasm? If we knew the answer to this question we might be able to cast the horoscope of a living being with certainty from its anatomical characteristics.

Very instructive in this respect is the question of the tenth free rib as a stigma of an asthenic constitution (Stiller). It has frequently been found in our parts of the globe that the occurrence of a tenth rib not reaching the costal arch is associated with a disposition of this kind (e.g., to pulmonary tuberculosis). What has been mentioned before with regard to the population of Switzerland [para. 39] should make us cautious in evaluating anatomical characteristics as stigmata, but it does not render it impossible, for we must first decide the question on what the difference in the norm (which actually exists if North Germany be compared with Switzerland) depends, and whether causes and conditions which produce attachment of the tenth rib to the arch are not the same as those which increase the resistance to tuberculosis of the lungs.

Unfortunately our knowledge of these matters, particularly of the connection between anatomical characteristics and susceptibility to disease, is very slight, and the chief reason is that hardly anything is known for certain about correlation of anatomical characteristics in cadavers. The whole investigation of stigmata and the constitution needs to be placed on a much firmer footing by the study of human cadavers (Hammar, Lubosch). Only a few results have at present been made known, but these few are full of promise and stimulative of further research. The problems can only be attacked by the collection of statistical material from the cadavers of numerous populations. Not until we know what characteristics in the body are correlative and which are freely combined, will it be possible to investigate the relations between the correlative characteristics, the composition of the population, the situation of life, and the disposition to diseases. But even now we can at least distinguish certain types by the external characteristics of the body (types cerebral, digestive, respiratory, motor, Bauer; pyknotic, Kretschmer) which can be placed in correlative connection with certain psychic dispositions [temperaments and mental diseases (Kretschmer)].

The material foundation of individuality exists in the germ-plasm of the individual [para. 32]. The reduction-divisions and the free combination of chromosomes are regarded by many as the foundation of permutations of characters, and the coupling of the genes within the chromosomes or the influence of a gene upon the development of many characters are regarded as a foundation of correlation of characters [para. 109]. In some way or other at any rate the germ-plasm becomes the foundation of the constitution. What is to be understood by the term "constitution" is not yet determined with certainty. One current definition calls constitution "the morphological and functional qualities of the individual remaining after the deduction of all qualities of species and race" (Tandler). But it is often very difficult to fix the boundary line between what is individual and what is racial. Constitution in the wider sense is thus equated to "inheritable composition"; it is the "original whole" of Kraus, but is at all events unchangeable and inaccessible to direct stimuli, the "somatic fatum" of the individual. Many also make a distinction between the inherited composition and constitution and understand by the latter rather a state of the body, sound in itself, upon which depends the more or less pronounced inclination to diseases due to external injurious influences (Martius, M. B. Schmidt); the alteration of the whole economy of the body by alcohol, for instance, or syphilis, is then termed constitution. This contrasts with the first view in being something acquired.

From the anatomical standpoint there is no doubt that the interpretation of the constitution as the sum content of all inborn characteristics is the correct one, all the more so since [paras. 72, 115] it is not the characteristics but the ability to develop characteristics which exists in the germ-plasm, and further because for the development of every characteristic there are certain limits of expansion within which the growth of the actual characteristic depends upon the development of the externals. Thus a susceptibility to diseases due to alcohol can only arise where capability of reacting to alcohol exists in the primordium; where this capability is wanting the susceptibility can never be produced by the influence of alcohol alone.

Before we can determine what the constitution is we must have a scale of comparison. Constitution and individuality form the only case which is subject to rule. This rule is for scientific thought the norm. Normality has to be placed next to individuality as its supplement. What is the norm and how do we obtain it?

Para. 44. In earlier times the word norm was often used in a twofold sense, and to-day it is always so used. The deep contrast between formal and functional interpretation, a contrast which permeates the whole study of organisms, appears again here inasmuch as "norm" is used on the one hand in the sense of "rule for anatomical results or findings," and on the other to mean "rule for the behaviour of a healthy human being." We can only be just to both interpretations by not attempting to regard either as alone valid while crediting the other with but little value. They must be accepted as actually existing side by side, and the importance of each for special problems must be recognized.

In order to express clearly this contrast as well as the different interpretations of the idea of an anatomical norm, the following table has been prepared. We have to distinguish:—

- I. Norma anatomica.
  - (*a*) Norma personalis (or unreal) subdivided into
    - (1) Norma statistica (Quetelet) and
    - (2) Norma intuitiva (Hildebrandt).
  - (*b*) Norma pluralium (or real). This is the Norma typum formans ("ideal," Lubosch), and comprises the Norma complexa (Rautmann).
- II. Norma functionalis (or physiological). This is only a norma personalis or norma responsibilis (Grote).

The following explanation of the table also illustrates the nature and significance of the idea of the norm.

The two meanings of norm become plain particularly in the contrasts they present; with rules we may contrast exceptions, but we may also speak of an abnormal man in the sense of a man who is diseased. In the first instance we have the pair of concepts: agreement with and exception to rules; in the other the pair healthy and diseased. A man may behave in a way quite exceptional to rule in the anatomical sense and yet not be diseased. Medical examination demands a norm which will enable a doctor to say whether a man is ill, but the morphologist wants a norm which will make it possible for him to say whether a finding obeys the rule or lies outside and beyond it (abnormal, anomalous). Pathological anatomy stands midway between the two, the pathologist recognizes no "diseases" but only "pathological findings." Numerous sections show diseased changes in organs in men who were healthy while living. Thus far pathological anatomy devotes itself to anatomical (formal) problems and seeks an anatomical norm, for the determination of a morbid change has sense only if a law exists for normal behaviour; in this connection it may be said that everything pathological is abnormal but everything that is abnormal is not pathological (e.g., an open foramen ovale in the interatrial septum of the heart).

The oldest attempt to obtain an anatomical norm is the construction of the "average man" of Quetelet. He applied numerical methods and the calculations of probabilities to individual variations of man and determined the average value for man's characteristics. His "average man" is he who shows either the mean value or one approximating very closely to it in all characteristics, while that which distinguishes each man from other men is a deviation from the norm. Quetelet's norm is a statistical one (mathematical norm, Rossle), for Quetelet naturally never dreamt of the actual existence of an "average man," he merely supposes him for purposes of comparison. But at least this much is certain, a single being, even if it be an imaginary one, is regarded as the norm; it is therefore a norma personalis. Apart from the impossibility of ever meeting this "average man" there are other fundamental objections to this conception of the norm which render it useless for practical purposes. Above all it is intended only for numerical characteristics—characteristics of form and position can be measured by an average value only indirectly. Since the most we can do is first to determine the frequency of certain forms and positions in order then to set up as an average value that form which occurs most frequently. So that a selection is made among forms, and those which are not selected must be regarded as abnormal without further consideration. The selection of the initial material is an unavoidable source of error in this determination of the norm. For since populations differ the norm of each must differ; and even within one population it will not be possible to avoid errors whether a selection be made or not. Baldness or short sight (Rossle) may then under certain circumstances appear normal or approximately so, or if a selection be made they may not appear at all (Rossle).

The conception of the norm proposed by Hildebrandt is very different. This may be called the intuitive norm, because it is not to be obtained by experience but by a mental process. Hildebrandt says that a norm cannot be obtained without an evaluation, and takes as the measure of value the individual incorporating the highest capability of performance in the species. In the "pure lines" of genetics the performance of the species and the individual coincide; in those species which are the result of amphimixis they are, however, different; the highest species-performance is according to Hildebrandt incorporated in individuals of complete "creative power," i.e., in heroes. He thus goes back consciously and emphatically to the ideas of Plato, with whom ideas are "the best models." This is perfectly true if we desire to judge the value of single individuals for the sum of all, but it leaves the needs of anatomy and medicine with regard to a norm quite unsatisfied. If we knew how the creative representatives of the species *Homo* were anatomically situated, we might expect to find in them characteristics which could certainly not be regarded as "laws" (pronounced development of the brain, hydrocephalus, phthisic disposition in a genius). Hildebrandt's intuitive norm, too, is unreal, since its starting point is a person; for the sum of individualities can never be contained in one person as a law.

An anatomical norm which also includes the individual case can therefore only be a multiple norm (norma pluralium), and further, it must be one which does not reject multiplicity of forms, but combines and includes them. Thus far the association with the theory of ideas is entirely justified, but a "primitive picture" upon which we can never look cannot be introduced as a scientific magnitude; the sum of the given multiplicity of forms must be regarded as the incorporation of the typical [cf. para. 26 and p. 142]. Here we have obviously an inner connection between the production of the individual and the limitation of a multiple norm. For both can be traced back to the origin of the most probable. Since, as we have already seen, the individual curve of all single characteristics of a living being and the curve of one single characteristic of all living beings coincide, since further probability forces the possible individual combinations into closer proximity about a highly probable value, we may interpret the sum of the most probable individvals as a norm of the single individual (Lubosch).

In this way alone is it possible to understand how any exposition of normal anatomy could be made. It has not been produced as the result of examination of innumerable single living beings on abstract lines. Historically and practically the method has been just the reverse. Vesalius, in spite of the paucity of cadaver material at his disposal, clung fast to types; Leonardo da Vinci deduced the mechanics and statics of the human skeleton from 37 cadavers, and his deductions were in accordance with truth (Sudhoff). To a great extent we have still to rely in the case of certain races of humanity and animals upon examination of very few examples which we could use to form conclusions, just as little as Vesalius his few cadavers for the construction of a normal anatomy, if there were not an inner connection between a single being taken at random and the norm. This connection lies within the area of statistically realized forms. Probability involves the supposition that probable individuals were included in the material examined. Of course, chance may play a different hand, and then errors occur which have to be corrected by subsequent researches.

This plurality of individuals, which includes the most probable combinations, is alone "actual" as a sum, even if it is not "real" in the sense of being present and given in every individual. That is impossible by the nature of the case. A norm of this kind includes many, theoretically all, characteristics with which anatomy in the widest sense has to deal. Closely akin here, too, is the morphological method of the older morphologists who attempted to delimit the type by seeking all attainable forms.

In practice the problem is a somewhat narrower one; for here we only require to know the norm of one or of very few characteristics in order that we may judge a characteristic of a given subject of examination. But it is clear that even for this narrower problem the norm must be a plural one, taking the sum of the most frequent values of this characteristic as norm. For this Rautmann has introduced the idea of the "greatest frequency value." This value (*D*) is that ordinate which indicates the average of the most frequent cases of a characteristic. Only with completely homogeneous material and therefore an entirely symmetrical curve does the ordinate *D* coincide with the mid-value (*M*); but the ordinate *D* passes through the peak of all the curves, including the unsymmetrical ones; in the curve illustrated the ordinate *M* passes through the value [13·29]. Rautmann's method enables us to answer the question, what characteristics (e.g., size of heart, chest expansion, pulse frequency) are the norm for men of a certain group, i.e., the correlation between these characteristics and other given group characteristics? Exact measurement of numerous individuals with respect to these characteristics is necessary, as well as reduction to space groups (fig. 4) and calculation of the results which are given in tabular form. With these tables a subject to be examined belonging to this group can then be compared. This method is very exact, but actually it is no more than the determination of the most probable combinations of one or more characteristics in very limited and extremely homogeneous material. The deciding factor in Rautmann's method is the condensation of large numerical areas into simple numbers and the frequency of the cases which are counted in one of these numerical areas (fig. 4). And this provides a special means for the determination of correlations. We can determine in this way what size of heart or what frequency of pulse belongs to a certain body size as greatest frequency value, with the proviso, of course, that the population must be highly uniform. This can be applied also to larger problems, to such questions, for example, as whether a certain musculature belongs correlatively to a certain shape of the nose, whether a certain attachment of the ribs and a certain condition of ossification belong correlatively to a certain form of the sternum. But for such questions as these we require gigantic numerical series. Clearness on this point is important. Much that seems to us to-day to be combined as in a mosaic might be shown on examination on a very large scale to be correlatively related by the method of greatest frequency value.

Every advance in our knowledge of the origin of the individual will also help us following what has been said, in delimiting anatomical norms. It is possible that we may some day be able by statistical methods to determine the correlation between a disposition to diseases and the constitution of an individual. At present that is impossible, since for a judgment of function, the harmony of the

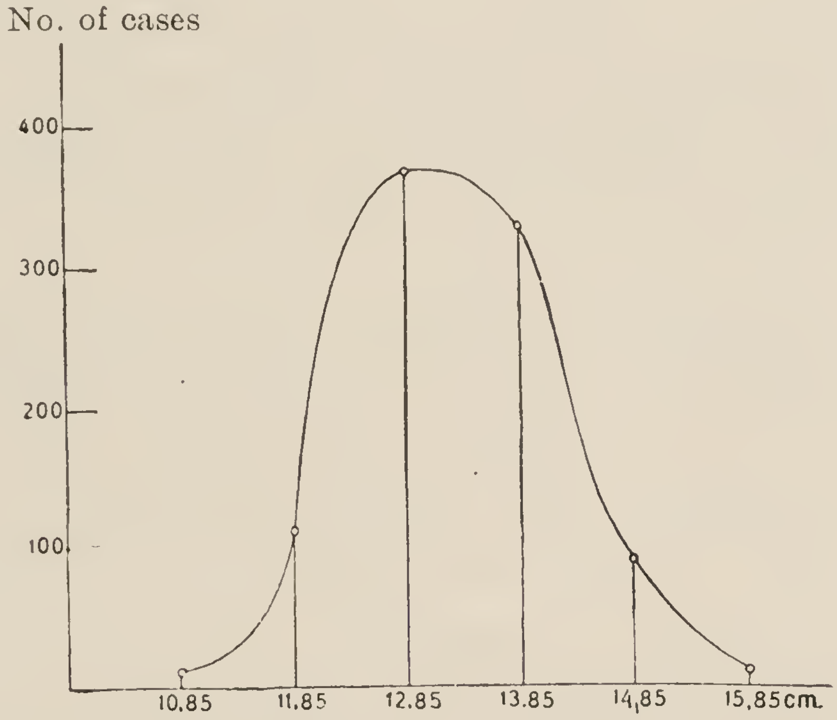

Fig. 4a.—Asymmetrical distribution of characters in a number of cases. The ordinate 12·85 is that of the greatest value. The ordinate of the mean value would be to the right through 13·29. (From Rautmann, l.c., p. 6, fig. 3.)

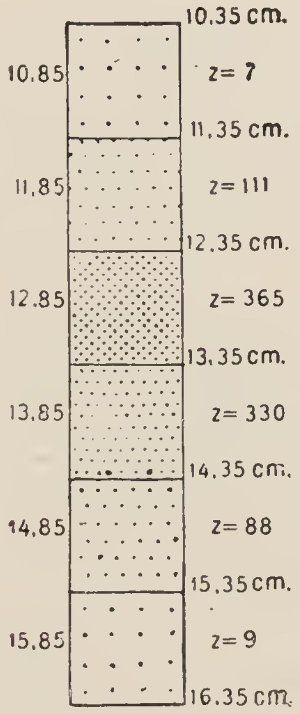

Fig. 4b.—Schematic representation of the distribution of the characters within definite space groups, for example, the size of the heart, in which the frames on the left indicate the value of the "reduced" group. Z = number of observed cases. Z 365 of the ordinate 12·85 does not mean that the size 12·85 was observed 365 times but that the group 12·35 to 13·35 occurred 365 times.

individual, the relation of all reactions to one another, the capability of regulation and adaptation are decisive. This totality, which empirically can only be comprehended in its parts and their effects, can anatomically be traced back to norms only by determining the norms of the parts. But this does not by any means imply that we have then found the norm of the cumulative effect of the parts forming the totality. For if the parts, taken singly, fall anatomically within known limits of probability, when united to form a whole they are a single isolated instance, so that a physiological norm is really a contradiction in terms (Grote). Normal life is possible even in a pronouncedly abnormal body, and indeed even with organs which have suffered pathological change. For the doctor, therefore, the physiological norm must be confined to the single being. Normality in this sense must mean "that the expressions of life of an individual correspond fully to his biological needs which result from the conjunction of the external situation of his life and his physiological possibilities of performance." "Man is the measure of his own normality" (Grote). Individuals may thus be classed as responsive and irresponsive (Grote), according as they can or cannot perform what is necessary to healthy life. Medicine thus has its own conception of the norm which it takes from clinical experience.

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(B) Morphology of Man as a Member of the Race.

(Racial Anatomy—Anthropogenesis.)

Para. 45. Correlative characteristics, i.e., those already existing in the germ-plasm, which can be deduced with such difficulty from the examination of given populations, reappear by inheritance, and can therefore easily be determined when there is an opportunity of tracing the path of inheritance. This is true of family characteristics and, above all, of those of the race. The essence of the race consists in the presence of a number of correlatively related inheritable characteristics. By their possession one race is distinguished from another. In the race we meet for the first time anatomical characteristics ranking above those of the individual.

Great caution is, however, necessary in deciding what is to be regarded as a racial characteristic, since we have to distinguish between real racial characteristics and that which is demanded by racial diagnosis in the narrower sense. That the racial element embraces very much more than this latter is beyond all doubt. It is a question not merely of a few but of a very large number of characteristics probably pervading the whole organization. The negroid, for instance, finds expression in the internal organs, in the brain, in the structure of the sense organs, no less than in the colour of the skin, the hair, the proportions, the nose and the lips. Of all such points very little is at present known. On the other hand, very few characteristics are used for racial diagnosis; indeed, a minimum suffices provided they are enough to distinguish one race systematically from another.

Caution is necessary, too, in dealing with other aspects of this question. First of all it is well to remember what has been said already (pp. 92, 93) as to features which are racially common. It is quite possible that a particular negro brain is not distinguishable from a particular Chinese brain. But it will not do to deduce from that there is no such thing as a negro brain or a Chinese brain, because racial and individual features overlap in all cases. The individual variations forming the multiple norms may be such that their total curves for two races partly coincide. In such cases we should only arrive at a racial diagnosis by determining the relations of the values of greatest frequency and by finding, for instance, that the frequency values of negro and Chinese differed, or that certain variations from the norm were more frequent in the one race, e.g., a sulcus lunatus in Sudanese negroes and Egyptians (Elliot Smith). And it must be added that we are as yet by no means clear as to the conditions regulating the formation of these norm limits. It must always be borne in mind that the organism inherits not characteristics but their primordia, in other words, that the degree of reaction capability is really the racial characteristic. If, therefore, the extent of this reaction is so great that it coincides within wide limits in all races, then the characteristic concerned can be no racial characteristic. The difficulties are rendered still greater by the fact that a considerable number of racial characteristics, too, are the result of or at least influenced by environmental factors. This is beyond doubt as regards shape of head and size of body. Therefore, if a typical negro and a typical Chinaman have brains which are to a large extent coincident in the general outlines of their structure, it merely means in the first instance that the primordium of like brain formation has existed in both races and that similarity results from the working o similar factors. But it does not mean that the primordium in both races is only capable of similar reactions under all circumstances. The one primordium might be capable of reacting where the other was not. This specific mode of reaction would then be the racial character in characteristics in general. We have to start with the phenotypes; our problem then is to deduce what is genotypical. We have always to remember that by racial characteristics we mean only what is genotypical in so far as it becomes visible in the phenotype. In so far as it is a sign of its genotypical origin, we can describe a certain characteristic as racial only in a positive sense, but in the negative sense we cannot without further qualification describe a certain characteristic as non-racial. For everything which appears phenotypically is ultimately genotypical. It depends solely upon whether on more exact statistico-biometrical investigation the reaction area of such genotypical primordium prove to be identical. Then it would not be a racial characteristic (see above). In any case it is plain that racial diagnosis is by no means so simple a matter as the enormous popular literature of the subject might lead us to suppose. We are quite ignorant as to how far men of different races may grow like one another in a like environment, i.e., much that we are apt to regard as racial may be due to phenotypical unspecific primordia. This is true less of the great primary races than of the numerous secondary, mixed races (see below).

All members of the three chief races [para. 28] show definite characteristics. But within each chief race the members of the races are again distinguished from one another by the varying degrees to which these characteristics are pronounced and by special inheritable features subordinate to the racial characteristics and occurring in groups (coarser and finer type among the Japanese and negroes, long-headed and short-headed negroes, etc.). These subdivisions are most striking within the white race, where they make it possible to define certain subraces (Nordic, Mediterranean, Oriental, Dinaric, Alpine, etc.) Man is thus clearly divided into three chief races, but these races are not in themselves homogeneous. This is due to two circumstances. In the first place, "pure" races in the strict sense do not exist at all; each of the three primary races has incorporated in itself older components and is the product of more complicated processes of racial formation which are no longer historically determinable. And secondly, racial formation has not stood still, in prehistoric as in historical time new secondary races have arisen (e.g., within the population of Europe). The most important racial divisions of Europe as they exist to-day can however be proved to have existed 10,000 years ago (in the later Stone Age), so that we can actually observe now only those racial phenomena which have resulted in historical times by intermixture of races and isolation of the products (e.g., the Jews, an "inheritable mixed race") and facial formations resulting from racial mixtures which, without isolation, have resulted in the formation of peoples (Teutons, Slavs, Celts, Hamites, Greeks, Turks, etc.). Insular position (the English), the effect of biological (social and cultural) isolation (the Jews), here disappears; cultural and linguistic community takes its place. For the causes of the formation of the races of man we are, therefore, obliged to have recourse to hypotheses. Intermixture and isolation can produce new combinations; something really new (colour and form of hair, colour of skin, etc.) can presumably depend only on genotypical mutations (thus perhaps the light skin colour of the Nordic race ? p. 160).

The racial formation of historical man, already completed (at any rate for *Homo europaeus*) by the later Stone Age, follows an older, prehistoric stage of multiplicity of races. This is a deduction from fossil remains found up to now almost exclusively in Europe but occasionally also in Asia and Africa. The oldest remains come from the boundary line between the tertiary and diluvial epochs. They are represented by the lower jaw of Mauer (Heidelberg) and the discovery at Trinil (Pithecanthropus). The lower jaw of Mauer is undoubtedly a human fossil and the oldest which we possess at present. The significance of Pithecanthropus is uncertain (ape, ape-man ?). The striking feature of this fossil is the extraordinarily low cranial roof with very pronounced supra-orbital prominences. The capacity of the skull is given as 600 cm. From the strata of the older Diluvial (older Palæolithic) epoch we have the discoveries from the Neanderthal, Spy, Krapina, La Chapelle, Le Moustier, Grimaldi, and perhaps others, the age of which is disputed (Piltdown, Rhodesia).

For this last skull, which has not yet been described in the textbooks, cf. Verhandlungen der Anatomischen Gesellschaft, 1924, and Mollinson.

Those first mentioned have in common a skull capacity below that of the lowest types of recent man, low cranial roof, receding brow, pronounced supra-orbital ridges, and the remainder of the skeleton possesses features which are not normal in recent man. In later diluvial times forms appear (Aurignacian) which do not differ from those of skeletons of recent man.

We may safely conclude that man had been racially divided into at least two chief races (Neanderthal and Aurignacian races), with intermixture between them (Oberkasseler ?) as early as diluvial times before he had established any permanent home, before the introduction of agriculture or the keeping of cattle, before the invention of pottery or the finer stone implements, possibly even before the discovery of fire. The Neanderthal race even is not a simple one; the Spy, Krapina, and Grimaldi (Negroid ?) discoveries show numbers of variations one with another and it is impossible to say whether they are of an individual or a racial character. No fossil remains have been found belonging to still earlier epochs. From the Tertiary period, from which we possess fossil remains of anthropoid apes, no human fossil is known as yet (1924). The question of "tertiary man" is therefore an open one. According to the one view based on the theory of descent, tertiary man is impossible (Schwalbe). Adherents of this theory declare that man has developed from a line from which come the chimpanzees; man must accordingly be more recent in the history of the earth than the anthropoid apes. Others hold the view (Darwin, Klaatsch) that man possesses more primitive features than do the anthropoids, and that the latter have specific characteristics which must have required just as long a period for their development as the typical characteristics of man (Darwin), so that both forms must be regarded as the final stages developed from common older stages. On these lines, the existence of tertiary man or pre-man is possible; flints (eoliths), believed to bear signs of having been worked, are regarded as traces of this man (Klaatsch). Others, however, declare these to be natural products, so that any definite decision as to tertiary man is impossible until positive finds from undoubted tertiary deposits are made.

Para. 46. In dealing with the question of the genesis of man we are therefore limited to conjectures. But with regard to "systematic" relationship it is certain that man stands nearest to the anthropoids, and in particular to the chimpanzees.

Blood-reaction tests have shown that serologically the blood-protein of man is most nearly related to the anthropoids, and particularly to the chimpanzees also. The "blood relationship" in this experimental sense thus actually exists (Nuttal).

But these observations make no pronouncement as to the genealogical relations between man and the other primates. These relations are certainly far more complicated than the usual genealogical trees would have us believe. If we are to have a clearer view of all this we must make a sharper distinction in anthropogenesis, as in the study of the formation of any other species [para. 32 ff)—between (1) the genesis of that germ-plasm to which human specific characteristics are due [their cause, para. 32] ; and (2) the appearance of those individuals which first deserve the name of man or pre-man. These two things must be kept apart here as in other cases.

As we have already seen, as far as our present experimental knowledge goes, and provided we do not assume quite different processes of species formation, germ-plasm changes are of "blind" (chance) origin in the individual. From this point they may be extended by amphimixis and thus reach the germ-plasm of numerous descendants. Whether this change at once produced a "man" phenotypically we do not know. But it is much more probable that it resulted in a "tendency to become man" (orthogenetically), that it spread by inheritance into numerous members of one population, and extended, as a result of the migration of the bearers, from its geographical point of origin, finally reaching later generations through amphimixis on both paternal and maternal side (become homozygotic). Thus it gradually led to the production of "pre-men" with a tendency towards further formation of the human type The unity of the specific characteristics of men can only be made comprehensible by assuming the spontaneous and single specific origin of a germ-plasm change. In respect of this formation of a human genus the origin of the human race is certainly homogeneous. According to the usually accepted view the first representatives of the species *Homo* were "many like and very similar" individuals in whose descendants pronounced differentiation led to the division into races. This is not very probable, for the reason that similarity is dependent upon like descent and, if it is not the result of mere chance, must lead to the absurd assumption of one single original pair. Much more probable and in agreement with our genealogical theories is the assumption of a given multiformity following and connected with an earlier multiformity. Every individual as a subject of examination is rooted deep in the past. We have to think of racial divisions of pre-man and primitive man and not of monophyletic (outcome of a first pair), but of polyphyletic (many groups of forms from older groups) origin.

The monogeny of the germ-plasm may be illustrated by the genealogical tree or divergence figure; the polyphyly of the phenotypes (men) by the ancestor-scheme (convergence figure). A combination of the two gives us a "net figure." The figure illustrates the assumption of the spread of the hominide germ-plasm within various races and enables us to understand how the phenotype man could appear in various places, and at the same time be racially divided, particularly if we assume migration, isolation and racial subdivision of pre-man. Many obscurities in racial anatomy are made more intelligible by this means, above all the fact that the three primitive races of man are not traceable one to another, but rather stand on parallel lines displaying the specific characteristics of man in three ways—that there are racial offshoots (Veddahs, Australians, Tasmanians), which are in many respects more primitive than these three races—finally, that within the human race characteristics exist which are referable to these diverse anthropoid forms or to an ape-form with which man decidedly does not stand in direct genealogical relationship. The following figure may serve to illustrate this (fig. 5).

The figure shows in the first line three races of chimpanzees (*a*, *b*, *c*) living in proximity to one another in an area of considerable size, as the orang-races do in Borneo (Selenka), or the herring shoals in the North Sea (Heinke). The signs +, ·, and × indicate the sum of inheritable racial characteristics (not individual). Each race comprises a population of individuals: 1, 2 are individuals of race *a*; 3, 4, 5 individuals of race *b*; 6, 7, 8 of race *c*. The individual 5 may be distinguished by the emergence of a mutational germinal change of a heritable kind furnishing the "tendency to formation of the hominide." This is assumed to have the power of transforming the constitution of the germ-plasm "towards man" wherever it penetrates and becomes active.

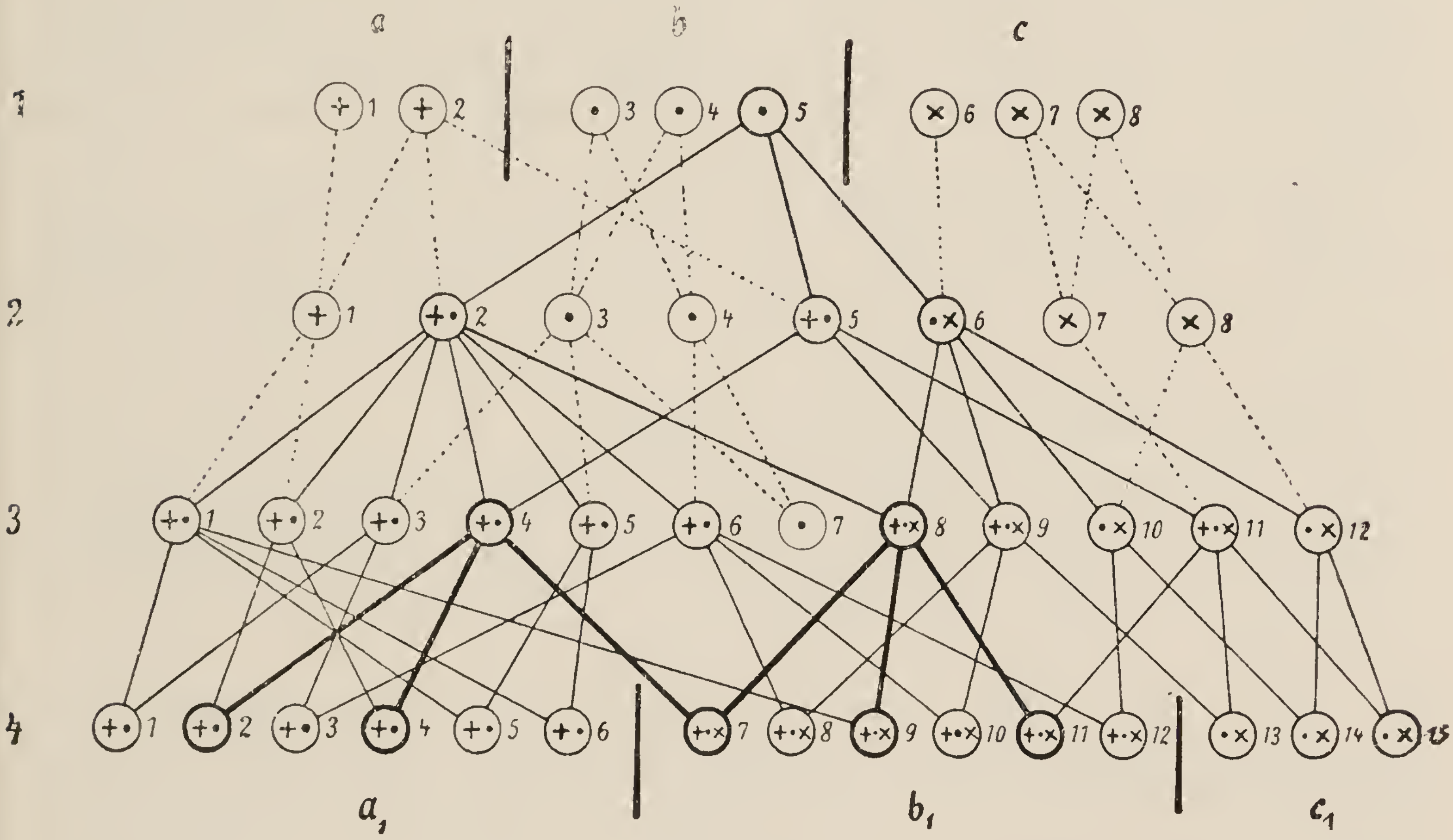

FIG. 5.

Rows 2 and 3 represent in simplified and exaggerated style migration and crossing of races. What actually takes place in the course of many generations and over wide areas is compressed in the figure into two generations, an earlier (row 2), and a later (row 3). The circles represent individual ("probandi") highly complicated, polyhybrid race-bastards. Among these we have 2^n new combinations of characteristics, which, provided we have pure segregation inheritance, always display the ancestral characteristics, but in a definite relationship (2^n) also form pure breeding combinations (with three pairs of characters, 8 of 64 possible combinations, with four pairs, 16 of 256). If such combinations are isolated they remain constant with regard to the characters thus combined. At the same time the expansion of the "hominide genes" proceeds, shown by thick lines. In row 3 the individuals, 4 and 8, are particularly emphasized as having received the altered germ-plasm from the two sides (homozygotous) and individual 7 which does not possess it at all and therefore embodies race *b* unchanged (provided no new combination independent of this appears in it).

Row 4 depicts the end of the process, which may extend over many centuries: the hominide stage with the beginning of isolation and race formation. The circles are probandi, possessing widely different genotypical constitution, according as they do or do not derive from forms 4 and 8 of row 3. The combination has produced the races +˙, + ˙× and ˙×, which, as the result of the possession of the hominide genes, display phenotypically to a greater or less extent the character of the human species.

If the whole scheme of $a_1b_1c_1$ be constructed above abc, and if the hominide genes be altered appropriately, e.g., to one for chimpanzees, and if the scheme be extended in a lateral direction, we shall get a picture of the relations of the initial races to the older primate form.

And here it becomes plain that it is only in this way that we can explain "cross relationship," i.e., the occurrence of like characters in those forms which are not connected "dichotomously" by ancestral lines, and which can never be connected in this way (see above). It occurred to Darwin to explain in this way many cases of parallel variation (pluripotent, Haecker). We must imagine the above figure, as has already been said, extended upward and laterally, and suppose single points replaced by a vast number of probandi, besides appropriately expanding the time involved in view of the complicated relations of the primates.

The "genus Man" may be described from the standpoint of descent as a starting point of single occurrence; looked at from the point of view of ascent it is veiled in obscurity. It has had a historical development; it is wide-rooted in older circles of forms and brings with it inherited predispositions. Human characters, then, to follow Klaatsch) are: (1) such as, inherited from older forms, existed before the development of man (i.e., derived from primordia of the primate germ-plasm); (2) such as arose with man (i.e., what can be referred to a single mutational change in the germ-plasm); (3) those which originated independently of one another with the development of man into separate races (i.e., which arose as reactions of the germ-plasm primordia to stimuli from life habits, possibly combined with further mutation changes of the primordia). It is to the second of these that the greatest significance attaches. This must be regarded as an "universal revolution of the constitution" (Haecker) which took place in the whole organization. And, accordingly, we must not assume that the human characters developed gradually in a heirarchic significance, such for example as erect position, change of the vertebral column, new position of the centre of gravity of the skull, changes of musculature, adaptation of the foot to the erect position, adaptation of the hand and the abandonment of locomotion on the four feet. Rather we have to suppose that the germ-plasm with its capability of typical reaction gave rise immediately to what was adapted, just as in the transition from aquatic to terrestrial life there can be no question of a gradual acquisition of adaptations one after the other, but only of an immediate functional adaptation to the newer conditions (pp. 57, 115, 116).

We must not omit to point out that this view of anthropogenesis has nothing to do with those systems of "phylogeny" which derive man from a number of anthropoids, and even from mammals, without proper scientific ground. Horst's system, for instance, is familiar. This derives Europeans from the pangolin via mulaka and chimpanzees, Negroes from armadillos via baboons and gorillas, Mongols from echidna via gibbon and orang-utang. These are fantastic notions with which science has nothing to do.

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(C) Morphology of Man as a Member of a Higher Category.

Para 47. Since the crosses between all the members of the same species are fertile there can be no doubt that all men are members of one species. But it is uncertain whether the oldest fossil human remains represent individuals of one species. In view of the fact that we may consider crosses between them and later (Aurignacian man) men to have been probable (Oberkasseler), it is possible that they ought to be regarded as mere races. Otherwise we should have to place them as distinct species alongside the existing human one. We should have then a genus *Homo* with the following species—*heidelbergensis*, *neandertalensis* (= *primigenius*), and *recens* (G. Schwalbe).

Since we cannot answer this question by the only decisive means, experimental crossing, it plays no part in science, and is in itself of secondary importance. It should also be pointed out that strictly speaking proof of sterile crossing between anthropoids and man has not yet been obtained. In nature, crossing between various species has taken place, generally with the result that further crossing between the bastard and the parent species has been impossible. The possibility of a fertile cross between man and the anthropoid apes may be admitted, but we may exclude the possibility that it would produce a fertile posterity in the same degree as that between one human and another.

Characters of species and genus appear in all men without exception. Their primordiæ must be present in the germ-plasm with such persistence that they assert themselves in every ontogenesis, unaffected by any crossing of germinal or somatic change. Anatomy based only on the characters of species would be extremely defective in many particulars (we may think of hair, skin, brain, thorax). Still more would this be the case, and to an increasing extent, if the characters of orders and classes were taken into account ; and yet this method of approach offers an indispensable supplement to individual or racial anatomy. For this provides the bridge between human and comparative anatomy, and not merely as the complement to what we already know from human anatomy, but as the necessary preliminary to all deeper insight into the nature of the structure of the human body. Anatomy thus treated is in the highest measure normative anatomy. This does not take the organs and the systems in their individualized form ; it even neglects the human norm, but seeks rather to show to what extent the universal features of the mammal and vertebrate organisms, and indeed of all metazoa, pervade the human organizations.

The following section is devoted to this point. We shall discuss the architectonics of the human body in the sequence prescribed by the material itself. First, depicting the architectonic characteristics which man shares with the metazoa (promorphological characteristics), then the general vertebrate characteristics from the description of which we derive our understanding of the division of the body into trunk, head, neck and limbs, as well as their inner structure. Next should come the descriptions of the systems, the organs of man from the standpoint of comparative anatomy ; this, however, must be neglected in favour of a special picture (cf. the Preface).

(1) Promorphology of Man.

(A) Antimerism.

Para. 48. Among the laws governing the body, none are of such fundamental importance as those of polarity and symmetry. If we draw lines joining the crown of the head to the buttocks, the right side of the body to the left, the ventral to the dorsal, we have the axes of the body, the longitudinal or main axis and the secondary axes. The planes marked off by pairs of axes are as follows: the median plane (main and dorsoventral axis), transverse (main and transverse axis), and horizontal (the two secondary axes).

Polarity is common to the human and to most animal and plant organisms. By this term is meant variety in the formation of the poles, i.e., of the ends of the main axis of the body. Most clearly seen in plants, one end of which is directed towards the light, while the other penetrates into the earth, in animals the poles are recognizable only in the construction of the axes and by the determination of the differences of each. An oral and aboral pole are to be distinguished in all.

The real inwardness and origin of polarity, which as a phenomenon is so familiar to us, is not yet revealed. A mutual influence of the atoms forcing them into an arrangement in a certain direction is one assumed cause which may take effect during development of the organism (Wilhelmi, Driesch). This reveals itself not only in the arrangement of the parts along the main axis, but also in the arrangement in the extremities where the terms proximal and distal are used to express the phenomenon. The polarity of the body is in general to be regarded as unalterable, but it can be reversed experimentally. It is well known that with plants the poles can be transposed. And with animals a change of polarity can be effected, accompanying the regeneration of lost parts of the body, e.g., by the growth of a head in place of a lost tail, or the development of a foot where a knee should have been produced by the regenerative processes. We describe this as heteromorphosis (Dürcken).

The mass of the human body is so arranged about the main axis that it can be divided into two halves by one single plane only, known as the median plane. These halves are not congruent and cannot be interchanged, but one resembles the other like the reflected image in a mirror. The corresponding points in each half of the body are approximately equidistant from the median plane, and every point within the body is in a constant fixed position with regard to the intersection of the co-ordinates of the three axes. This form, too, the real character of which causes much speculation, is a feature shared by man with many animals and plants which are generally termed ' bilateralia," although this name is not completely exhaustive and gives no hint of possible subdivisions.

In those cases in which the body can only be subdivided into two halves by one plane great variety is still possible, according as the result gives two or more corresponding portions on each side (antimerism) and according as these antimeres are merely similar to one another or congruent. This is dependent upon the arrangement of the axes and their mutual relationships. Fig. 6a shows a bilateral symmetrical arrangement with four antimeres congruent in pairs. The stereometric basal form here is a rhombus with equal sides, on which pyramids are erected. The secondary axes are equal in length. But the surface upon which the human body is based is an isoceles triangle (Haeckel), upon which stands a pyramid cut off below its

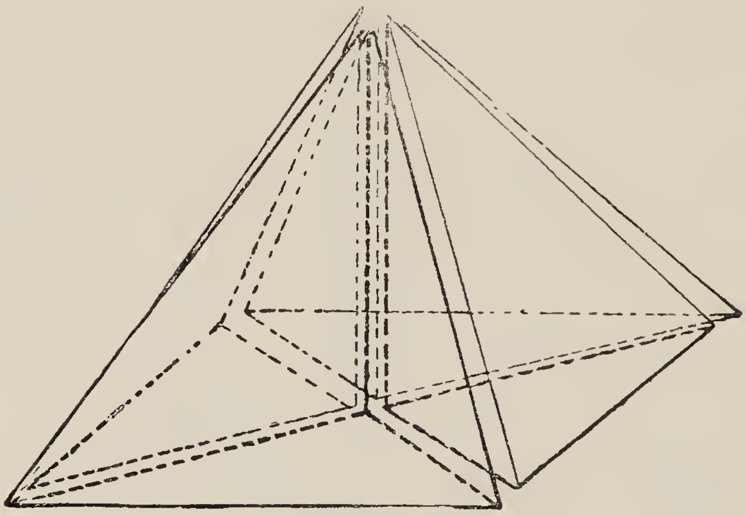

Fig. 6a.

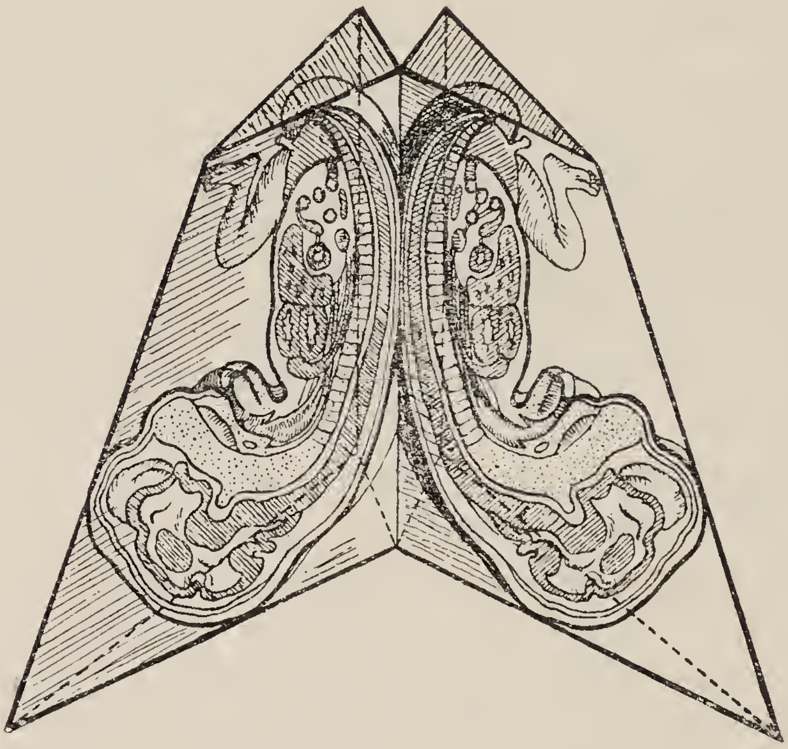

Fig. 6b.—A pyramid minus the apex, is erected on an equilateral triangle. The body enclosed in the figure is outlined, the pyramid bisected and the halves separated.

apex, as in fig. 6b. In the figure the two halves of the body have been separated in such a way that the two right-angled triangles making up the isosceles triangle forming the base of the pyramid may be seen. In this construction we distinguish the main axis with the two different poles (the cranial pole and the anal pole) and the secondary or transverse axes perpendicular to the main axis, unequal to one another in length and not bisecting the main axis.

For beings of this kind of bilateral symmetry Haeckel invented the name "zeugites," which is intended to convey the fact that in these cases two connected similar single beings have formed a new joined being. In fact, more recent investigations have shown that each of the two halves possesses at the stage of the first division of the fertilized egg a high degree of independence [c.f. later, para. 87]. E. Haeckel long ago pointed out that in all technical mechanical contrivances for motion the principle of "zeugites" was embodied. The distribution of mass and the narrowing of the body towards the poles is obviously of advantage in overcoming resistance in water and air. All our contrivances for movement on land, in the water and in the air are zeugites.

While the front and hind portions of the body, the ventral and the dorsal surfaces, are highly dissimilar, the two halves separated by the median plane are approximate antimeres. These two antimeres are termed the right and left, and each possesses such striking functional peculiarities that there are even what have been called "right and left" men. The greater cleverness and muscular strength revealed in right-handedness is matched by the superior sensibility present in the left side. The mirror symmetry that exists in general is never a functional (physiological) symmetry. It has been proved that, physiologically, considerable differences exist in the possible output of strength between the two sides, so that the movement of the body if it takes place without deliberate intent (as, for instance, with animals under pursuit) never results in progression in a straight line, but must produce a spiral movement corresponding to the greater influence of one side of the body (Guldberg).

Not to be confused with the morphological distinction between right and left is the physiological idea of right and left, which in many people is incompletely developed, or wanting altogether. Such people lack to a greater or less degree the ability to distinguish right from left (Elze).

But morphologically, too, the symmetry of the body is only present in the broadest outlines—in detail the human body presents a decidedly unsymmetrical picture. Knowledge of these asymmetries is of equal importance to the doctor and the anatomist, and this particularly because they follow certain laws and in large measure help us to understand topographical anatomy. We may speak of external and internal asymmetries.

External Asymmetries.

Para. 49. Reckoning from the median line outwards the one half of the body is always different from the other. Organs of like significance, such as the nipples, the eyes, halves of the nose, are always at different distances from the median line, or at different heights. This is true to such an extent that it is not correct to speak of symmetry at all in the strict sense, and the two halves of the face for instance display widely differing proportions.

It is a striking fact that the artists of antiquity recognized this at a very early day, and the most beautiful statues, e.g., the head of Venus of Milo, show this asymmetry (Plasse), which, we must admit, actually forms a considerable part of the charm of the face. It seems to be the case that what attracts us in a face is this very irregularity, while, as Plasse puts it, complete regularity may be beautiful, but would at the same time appear "uniform and uninteresting."

In points of detail measurement has shown the typically unequal portions of the eye, nose, mouth, zygoma, and even of the fundamental parts of the bony skeleton, the orbits, bony and cartilaginous nose, individual parts of the skeleton of the face and cranium; in some men it is the one and in others the other half (generally the left) which has the higher values. The same is true of the neck and trunk (Hasse).

To this must be added certain peculiarities of the limbs which are not fully explained by what has just been said. The asymmetries already mentioned do not owe their origins to use or special static influences. Rather is it probable that they are the expression of formatively different primordia which were present in the ovum. Possibly they are the expression of constricting influences during intra-uterine development. Little is known as to this. The facts as to the extremities are otherwise. The most noticeable difference here is one between left and right; the right arm is generally longer and thicker than the left and the left leg longer and stronger than the right. Whether a pair of boots fit can normally only be decided if the left boot is tried on. In this case all the parts of the trunk appear broader and deeper from the front to the back, on the right than on the left. The weight of the right half of the body is also greater than the left. The centre of gravity lies towards the right. Occasionally, however, the case with regard to the limbs is exactly reversed. All this depends not only upon differences of growth, but is attributable to formal asymmetries of the vertebral column (Hasse). The vertebral column seldom stands in the median line. It is almost invariably situated, as a physiological scoliosis, to the right or left. If, as happens in the majority of cases, it is inclined to the right in the chest, then in the cervical region and again in the lumbar region it will tend toward the left. The result is a lowering of the right shoulder, a higher position of the right ilium, so that the right arm must appear longer than the left. Where the inclination of the vertebral column is reversed, the reverse is true of the extremities. Of the causes of these peculiar curves in the vertebral column we know nothing. As we shall see in a moment we must add to this explanation of the difference in the length of the extremities something else which will explain their varying thicknesses.

Internal Asymmetry.

A distinction may here be made between those organs of the body which exist in pairs, and those which do not. Organs existing in pairs, cerebrum, organs of sight, of hearing, salivary glands, lungs, thymus, kidneys, suprarenals, gonads, even the ribs and the sternum, though having a like ground plan differ in form on either side ; this is apparently, e.g., in the case of the lungs, a result of development within variously shaped spaces. But quite apart from the fact that this raises the question of why these spaces are themselves different, this asymmetry is at any rate inherited, since it is visible in the earliest primordium of the lungs as a small sprout on the anterior wall of the gut (Bender, Heidenhain, Heiss). The question here, and in similar cases, is not how the asymmetry arises, but rather how the very rare symmetry of the lungs can come into being at all. In other cases, such as that of the suprarenals, a mechanical explanation of the form seems to be only partially accounted for by spatial restrictions, e.g., this would explain the inferior margin of the lower lobe of the right lung. The differences in form are, however, indicated in the primordia of both suprarenals.

In practice the most important symmetry of organs existing in pairs is that of the cerebrum, where different degrees of development are present on the right and left sides, in parts which are alike in general principle. This is particularly evident in the superficial area known as the speech centre in the region of the third convolution on the left side. But this distinction applies not merely to the speech centre ; it extends over the whole motor zone in such a way that with the decussation of the nerve paths we get right-handedness in man, which is in all probability a “ left-brainedness.” On this point there are individual divergencies (left-handed people). As a result of this functional difference we find that the right anterior extremity, which has greater functional demands upon it, is thicker than the left. So that in addition to the above-mentioned apparent increase in length we have an actual asymmetry of thickness. Of the hinder extremities, the left, or longer one, seems to be preferred for standing and therefore to be thicker. Although there is not complete unanimity of opinion on the point, it is a remarkable fact that man is, as a rule, "left-legged" (e.g., stepping off with the left foot when marching). In this combination of right arm and left leg we see the cross-movement, which is common in quadrupeds reproduced in man. From the point of view of purpose, this type of movement enables the quadruped to maintain a horizontal position of the body, even when in motion.

As to the causes of right-handedness, we are still completely in the dark (Gaupp), although the asymmetry of the aortic arch with the better nourishment of the left half of the brain has been called upon as explanation. The weightiest objection to this is the fact that left-handedness does not by any means necessarily occur with *situs inversus*, as it would have to do in accordance with this theory. In mammals and birds which have been experimentally observed a difference in length of right and left limbs is said to exist (Guldberg, Mollison), but it is still uncertain whether right- and left-handedness exists in animals. It is possibly that this is a human characteristic.

The pairs of sense organs of the head occupy a special position. They display the mirror resemblance in its purest form. The one eye is in all its parts the complete *situs inversus* of the other. If we look at the complicated nerve supply, by means of which the conjugate movements of the eyes are brought about, and at the optic chiasma, it is impossible to imagine that this whole mechanism has arisen from the division of a single (cyclopic) primordium. The central compensation of the antimerism of the bulb and its muscles, as it appears in the co-ordinated movement of the eyes, decussation of the oculomotor fibres to the rectus internus, uncrossed path of the abducens (rectus lateralis), is from the standpoint of adaptation so difficult a problem that it seems impossible that it should become intelligible on these lines.

With the sense organs of space, things are very similar. The arrangement of this organ, e.g., the horizontal semicircular canal, is such that each, being the mirror image of the other, receives opposite stimuli which can be so interpreted by the brain that they are summated, whereas if they were congruent the stimuli of the two sides would cancel each other's effect. When the head is turned to the right the endolymph in the right horizontal semicircular canal flows towards the ampulla and stimulates the cupola = strong nystagmus towards the same side, i.e., the right; in the left horizontal semicircular canal, with the same movement of the head, the endolymph flows towards the non-ampullated extremity and stimulates the cupola = feeble nystagmus towards the opposite side, i.e., to the right side. Both effects are strengthened.

Extensive asymmetries are finally seen in the axial skeleton (one-sided development of the cervical ribs, thirteen ribs, transitional vertebra, a sacral vertebra on one side and a lumbar vertebra on the other, etc.). Each side of the axial skeleton may vary independently, and there may even be more vertebræ on one side than on the other owing to the presence of a supernumerary vertebra (cf. Fischel and Stieve).

Most of the unpaired organs of the body have originated in a paired primordium. This is even true of some parts of the skeleton, e.g., the sternum, which is produced by fusion of paired rib arches. Even the heart is originally entirely and the aorta partly paired in its primordium. The only organs unpaired from the beginning are the alimentary canal, the urinary bladder (this only in its entodermal portion; the trigone has a paired primordium) and the inferior vena cava. But the gut and the inferior vena cava are situated in the median plane from the beginning, and it is only in the course of development, though admittedly at a very early stage, that a displacement occurs.

The first displacement which can be observed is that of the liver towards the right and of the endocardial tube to the left; the latter takes place in the chick as early as the third day of incubation. The details are as follows:—

The gut, at first situated symmetrically in the median plane of the body, moves later with its cranial part (the œsophagus) towards the left, so that it becomes visible and accessible below the larynx on the left side behind the trachea. The gut consequently crosses the left bronchus and penetrates the diaphragm to the left of the aorta. The stomach lies on the left, the duodenum on the right side of the abdomen; the jejunum usually lies on the left and the ileum on the right. Of the large glands of the intestinal canal the liver, at first symmetrical, moves wholly to the right, the pancreas to the left; the spleen is displaced entirely to the left. All these displacements which take place during the first fœtal period (up to the third month have far-reaching effects upon the development of the viscera of the thorax and of the abdomen. While, for instance, the liver develops its right lobe to a pronounced degree and causes its convexity to become attached to the upper and posterior wall of the diaphragm, the bursa omentalis, the cause of so much difficulty to the student, is developed in conjunction with the displacement of the stomach to the left (cf. fig. 57).

In the organs of the thorax similar but not quite such extensive alterations take place. The heart enters the left half of the thorax. As a result, the left pleural cavity is narrowed in a transverse direction while the right half becomes wider but is reduced in height by the development of the liver. The ascending part of the aorta, originally situated in the middle line in the front part of the neck, sends out the branchial arteries, six in number, like an arcade around the pharynx dorsally and there they unite into a longitudinal stem (aorta descendens). The series of arches becomes decidedly asymmetrical, inasmuch as one, namely, the fourth, develops on the left into the aortic arch, while the large branches of the aorta are produced from the original arch series. This again is of far-reaching effect on the topography of the viscera (position of the aorta to the left of the vertebral column, relation to the left bronchus, greater length of the right intercostal arteries, course of the innominate artery from left to right in front of the trachea). The position of the right auricle being more favourable for the reception of an increased amount of blood leads to an enhanced development of the superior vena cava on that side.

The original left superior vena cava conducts its blood through an anastomosis to the right superior vena cava. This anastomosis becomes the left innominate which originally opened into the coronary sinus (remnant of the duct of Cuvier). This remnant of the duct of Cuvier perishes; it can, however, persist. By the position of the heart the vena azygos major also reaches a greater development; the left, originally symmetrical with it, is partially absorbed in it and thus becomes hemiazygos. The displacement of the liver towards the right also carries the portal vein to the right. The course of the inferior vena cava on the right is the cause of the termination of the left spermatic vein in the left renal vein.

Not only do simple displacements take place, but also torsions of the unpaired intestines. The heart turns about its longitudinal axis towards the left and thus turns its right surface towards the front. The twistings of the mid-gut are very complicated. All this influences the course of the nerves (left phrenic deeper in the mediastinum than the right; left vagus in front of the alimentary canal, and on the anterior surface of the stomach, the right vagus behind the gut and on the posterior surface of the stomach). Finally, mention must be made of the asymmetry of important nerve trunks due to asymmetric formation of terminal or intermediate areas (left vagus to the liver, the right to the gut, left recurrent nerve in the neck deeper than on the right because it has to go deeper around the aortic arch in contrast to the right recurrent which winds round the subclavian artery on the surface).

In rare cases the whole of the asymmetry of the body is reversed. What is normally on the right appears on the left and vice versa, so that the opened cadaver resembles the image of a normal cadaver seen in a mirror. Not only are the grosser relations reversed, but even the deviations in the course of the nerves and vessels are changed about down to the smallest details (*situs solitus* and *situs totalis*, also called heteropositus viscerum). While *situs inversus* of single organs, e.g., the heart, must be reckoned among the malformations, complete *situs inversus* is not so, but a variety of formation which is certainly much rarer than other varieties of normal *situs* (literature in Schwalbe). A large number of cases of *situs inversus* are known. In recent times they have been recognized more frequently during life. (The heart beats on the right, the left ventricle stands higher than on the right [a sure sign of *situs inversus*], X-ray pictures of the intestinal canal.)

Para. 50. The asymmetries seen in mammals and in man are of small extent when compared with those of the animal kingdom in general (Brandt, Haecker, Rabl, Theel, Werner). Asymmetry actually appears to be the dominating principle.

Asymmetries of the whole body are seen in the highest degree in snails with their right- and left-handed spirals; displacements and torsions of the gut and its adjuncts are commonly present. More pronounced development on one side of the lungs and sexual organs in the case of long-bodied creatures (amphibia and reptiles) is familiar; the same may be said of displacements whereby one gonad lies in front of the other (snakes). One-sided development may be carried to the point at which the other organ vanishes (sex organs of birds, Stieve; cf. for all this Werner's summary). Mode of life and carriage of the body produce asymmetries of form, as in the case of Amphioxus; the best-known instance of this is Pleuronectes (flounders).

Since K. E. von Baer, numerous suggestions have been made as to the origin of asymmetries, such as the position of the embryo on the right of the yolk sac, caused by the left-hand position of the heart, curves of the embryo, restrictions of space (cf. Brandt, Haecker, Werner). This leads logically to the question of the nature of symmetry and asymmetry and the relation of antimeres to one another. Have there ever been completely symmetrical "zeugites," and is the asymmetry, which may now be regarded as the rule, something which has developed or something which was inherent? That the former is, at any rate, partially the case is demonstrated by pleuronectides, and on a superficial examination it seems impossible to avoid the conclusion that restriction of space and prolongation of the body, as in snakes, have produced asymmetries. But it must be remembered that this is only an increase of the universal asymmetries which appear to be inherent. Phylogenesis here brings us up against certain limits, inasmuch as though we do find everywhere an increase of asymmetry we never see complete symmetry of the whole organism. Ontogenesis takes us far but not far enough completely to solve the riddle in which antimerism of the "zeugites" is hidden. But ontogenesis does enable us to recognize that symmetrical relations of the developed organism are often already present in the ripe ovum (O. Schultze, Rabl).

This fact appears most remarkably in snails, with their high degree of asymmetry (Rabl); the mature ova of snails possess a spiral aster and a spiral arrangement of the protoplasm. The direction of these spirals coincides with that of the spirals of the shell of the fully developed animal; in other words, it runs in the egg either to the left or to the right, so that we may conclude in this case, with a strong degree of probability, that the molecular components forming the egg-plasm have a spiral structure.

Schultze has proved bilaterality in the unfertilized frog's egg; hence we may assume that the plane of symmetry is foreshadowed in the unfertilized egg by distribution of materials and mutual influences of the elementary parts, let these be what they may. The entrance of the sperm does not seem to be necessary for the production of a definite distribution of the egg materials, and the fixation of the plane of symmetry does not appear to depend on the site of entrance of the sperm, since parthogenesis produces symmetrical forms (Driesch).

The question whether the first cleavage of the egg is connected with the later median plane arises here. There are cases where a connection does exist; in these the line of division does actually separate the material for the right and left side, and this first cleavage plane lies in the same plane as the track which was traversed by the sperm as it penetrated the egg. In such cases it is probable that the symmetry is already present in the unfertilized egg, or it becomes so under the influence of the entry of the sperm. In the normal course of fertilization we may assume that it is not the function of the sperm to supply this stimulus, but rather to enter the ovum at the already existing plane of symmetry (O. Schultze). But the fact that the sperm does under certain circumstances exert an influence that upsets the normal arrangement is demonstrated by experiments in which the sperm is introduced artificially at a certain spot in the egg, and the first cleavage then occurred at the plane in which the sperm entered. Our question then cannot always be answered in the affirmative; many well established cases are known, besides, in which the first cleavage plane has no relation to the planes of symmetry; in these cases the symmetry of the unfertilized egg is not apparent, but develops later.

Symmetry, or better, the peculiar nature of the structures leading to the symmetry of the future organism, appears to be subject to influences at a later stage too. It is possible by destroying at one point certain components of the egg, at the stage of the formation of the neural tube, for instance, to change the whole situs, e.g., to produce *situs inversus* (Spemann, Wilhelmi). All this shows us that the "bilateral structure" of organisms, which we may picture to ourselves as like the subjection to the law which reigns in crystals, is not, as it is in crystals, something rigid and unalterable, but rather fluid, active, possibly of such a kind that the parts are in some sort of equilibrium which can pass over, after displacement of the particles, into a new state of equilibrium.

We are, however, still quite in the dark as to the effect of these forces or the influence exercised by one side or the other.

The experience gained by causing Nature to form anew an antimere which has been destroyed is important. This has been done with the eggs of amphibia [para. 87], with the result that after destruction of one of the cells of the first division half an embryo was produced, and this completed its antimere by new formation from the remnant of the cell or by new formation where complete isolation had been effected (post-generation, Roux). And the control of symmetry has been observed ingeniously in the completion of the small bony parts, in themselves symmetrical, or occasionally unsymmetrical, in the skin of echinoderms (Wilhelmi). From the phenomena observed in all these processes the conclusion has been drawn that symmetry and polarity represent a kind of dependent growth of such a nature that a given particle is able to exert a directing influence upon neighbouring particles. Stimuli are said to accompany polarity, which cause something different from what is already there to appear, while with symmetry they originate something that is like what is already there. This seems to be confirmed by the remarkable phenomenon of secondary symmetry (Bateson) which we have not yet mentioned, i.e., the process which transforms a human hand into a form symmetrical in itself (six fingers, each three arranged about a plane of symmetry, etc., Wilhelmi).

Here the directing stimuli appear to come from the fingers already existing and are apparently able to exert an influence when, as a result of variations in the primordium of the hand, the normally dominant polarity and symmetry are weakened. In this case we might think of the normal arrangement as a combined effect of the stimulus of polarity and symmetry balancing each other. But here we have to deal only with one theory of symmetry, and according to this theory it can be regarded as the expression of directing stimuli of varying strength. According to this each antimere would have a share in determining the future position of every organ. Complete symmetry would arise when the direction stimuli on both sides were of equal strength; when the stimulus on one side was completely absent we should have the maximum asymmetry.

But this does not answer the question of the formal value of antimeres; for symmetry is thus the outcome of two given autonomous stimulus-bearers acting counter to one another, not as in experimental conditions the effect of growth stimuli alone. The question of *situs inversus* may perhaps avail to solve this difficulty too; on this matter important researches have recently been made. It has been shown that in double formations united at the tail the anterior ends often possess opposite *situs*, and that usually but not always the right one has the reversed *situs* (Spemann). Rauber was the first to draw attention to the fact that between a double formation and a complete twin-formation there are differences of degree alone and not of kind. He actually compares the vertebrate with the animal colony (page 51).

The first cells of the dividing egg, even when separated, as is well known in the case of sea-urchins, possess the power of producing whole embryos of one-half or one-quarter the normal size. Apparently the origin of twins from one egg may be traced to a separation of the cells of the first division for mammals and man [cf. para. 78]. The normal polyembryony of the armadillo, where four and eight derivatives from one egg are the rule, should be mentioned here. This is a true colony formation.

We might thus look upon the bilateral organism as a stem of two beings, each half as virtually a twin, but each capable of becoming independent under certain conditions. Thus a man with *situs inversus* might be regarded as the right hand of one of two twins from one egg, of which the left hand one had perished very early, possibly at an early stage in the division of the egg. Each virtual twin would have to be regarded as the bearer of direction stimuli of varying strengths, the combined action of these producing the asymmetry of the body. Why the one half normally forces the gut to the left and the other the liver to the right remains obscure.

We are overcome by a problem of great difficulty in considering this far-reaching autonomy of the antimeres in respect of form when we think of their connection by means of the nerves. The innervation is so arranged that the right-hand side of the body is served in general from the left-hand side of the brain, and vice versa. The fact that most nerve paths are crossed in the median line has not yet been explained by any theory or hypothesis; this crossing is just as deeply based in the organization as bilateral symmetry (cf. Jacobsohn-Lask).

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(B) Metamerism.

(Segmental Anatomy of Man.)

Para. 51.—In addition to antimerism, the human, like the animal organism, is subject to a second architectonic principle, which is of supreme importance for a scientific understanding of anatomy. We are, in fact, able to demonstrate that the body consists of a series of successive portions arranged in polar order, each of which originally has a share in all the chief systems of the body. The serial portions (segments, metameres) contain at an early stage of development a definite portion of the skeleton, musculature, vascular and nervous system, urinary organs, and even of integument. Only in the alimentary system in the vertebrates is a division of this kind, at least in the trunk, undemonstrable (for invertebrates, cf. fig. 11). In the adult body there are regions in which this vertical division is obvious even to the beginner; the most obvious example is the vertebral column, whose single elements repeat one and the same type, differing only according to its region. In the region of the thorax, in particular, we see in the ribs, intercostal nerves, and intercostal vessels metamerism in its pure form. The beautiful regularity we see in preparations of the long muscles of the back, with the posterior primary divisions of the spinal nerves, depends on the metamerism which is completely preserved in the deeper levels (rotatores) and still persists in the superficial layers through origins and insertions and innervation. But the division of the straight ventral muscle and the form of the deep muscles of the neck (M. longi and Musculi scaleni) are based on similar metamerism. It can further be shown that in addition to these places, where it is obvious, metamerism is present where the naive observer would not look for it, and knowledge here is the key to many secrets of human anatomy. We shall demonstrate these metameres, first of all, in the trunk only, while those in the head and limbs will be discussed later.

Para. 52. The developmental processes connected with the mesoderm provide an insight, too, into the origin of the metamerism of the body. For metamerism is linked in the first instance with the mesoderm and with the organ formations proceeding therefrom: somites, urinary organs, as well as mesenchyme and its differentiations (skeleton, blood-vessels, sclerotome). This may be called primary metamerism in contrast to secondary metamerism, which under the influence of the myotomes in particular finds expression in the nervous system.

The division of the mesoderm is effected by a transverse and longitudinal splitting (fig. 12, a and b) in such a way that transverse constrictions first of all divide the dorsal region into separate successsive segments (somites). This division always begins at the front and progresses towards the back so that the oldest somite lies behind the head region. Posteriorly an undivided area is left from which, as it were, young somites are split off. Following their vertical division comes a horizontal one, producing the ventral boundaries of the somites. From these somites the elements of the wall situated medially next to the neural tube are transformed into muscle fibres of the body (myotomes) while the remainder produce connective tissue. The myotomes are separated from one another by tissue representing primary tendons (myosepta). The myotomes situated next to the neural tube form the starting-point of the dorsal musculature of the body, while ventral downgrowths provide the basis of the ventral trunk muscles which develop later. The spinal nerves divide accordingly into a dorsal and ventral branch.

This provides an explanation of the behaviour of the nerves which come into immediate proximity with the myotomes of the spinal column, unite with it, forming motor terminal plates, and in future remain indissolubly connected with it. In the more primitive vertebrates the myotomes cover the whole lateral wall of the trunk (Langelaan) and are here distinguished by numerous windings and folds, so that, particularly on the ventral side, the myotomes run obliquely to the longitudinal axis of the body. As a result the nerves enter myotomes to which they do not originally belong, and accordingly we get at least a bineural innervation in contrast to the dorsal myotomes which invariably have a mononeural innervation (Maurer).

The nerve fibres running into every myotome originate in the

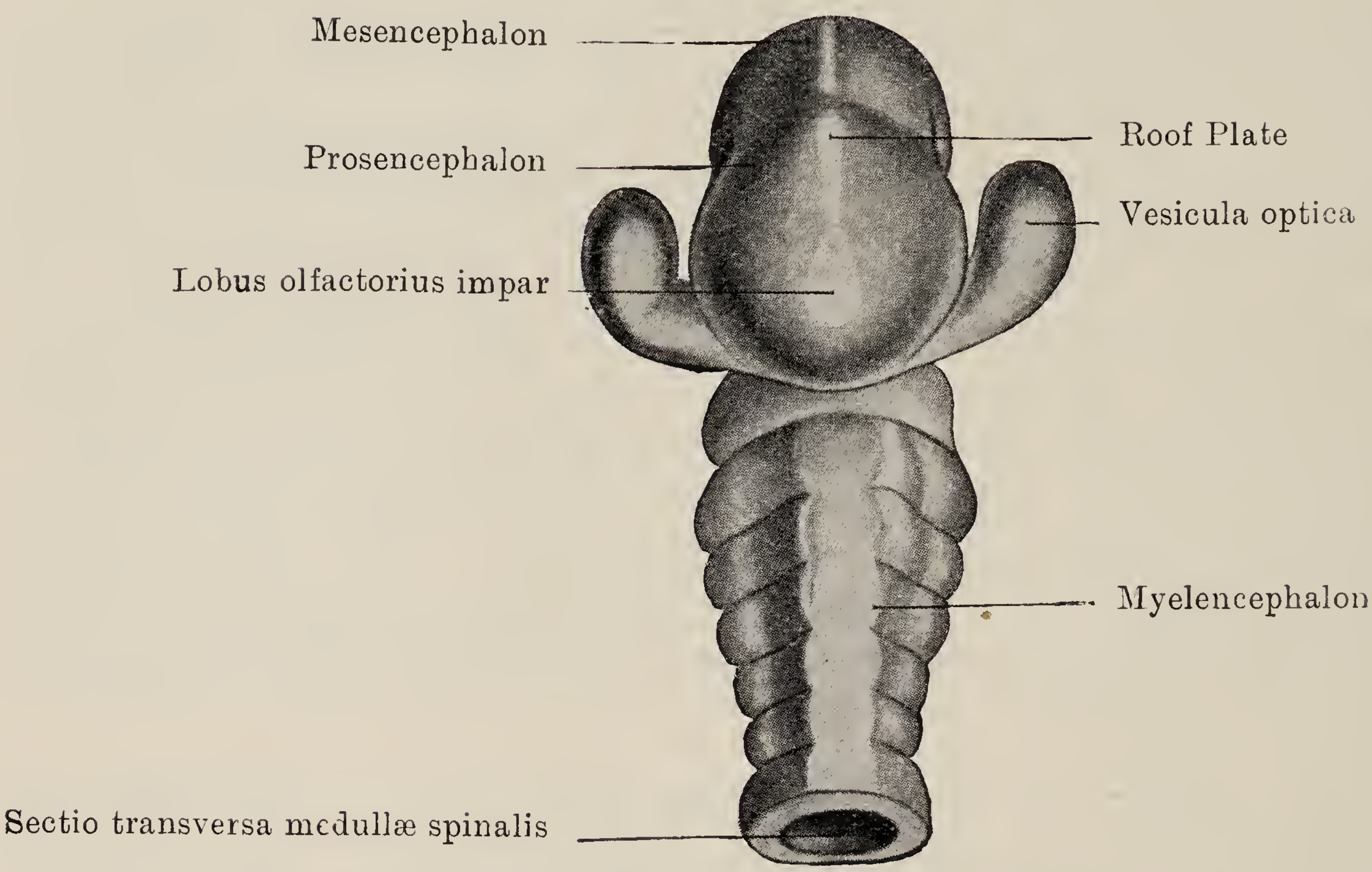

FIG. 7.—Neuromeres. Ventral aspect of the brain from a sheep embryo of 4 mm., wax reconstruction enlarged fifty times. After Neumayer from Kollmann's "Hand-atlas of Human Embryology," vol. ii, fig. 634. (Jena, Fischer, 1907.) The five neuromeres of the myelencephalon are visible.

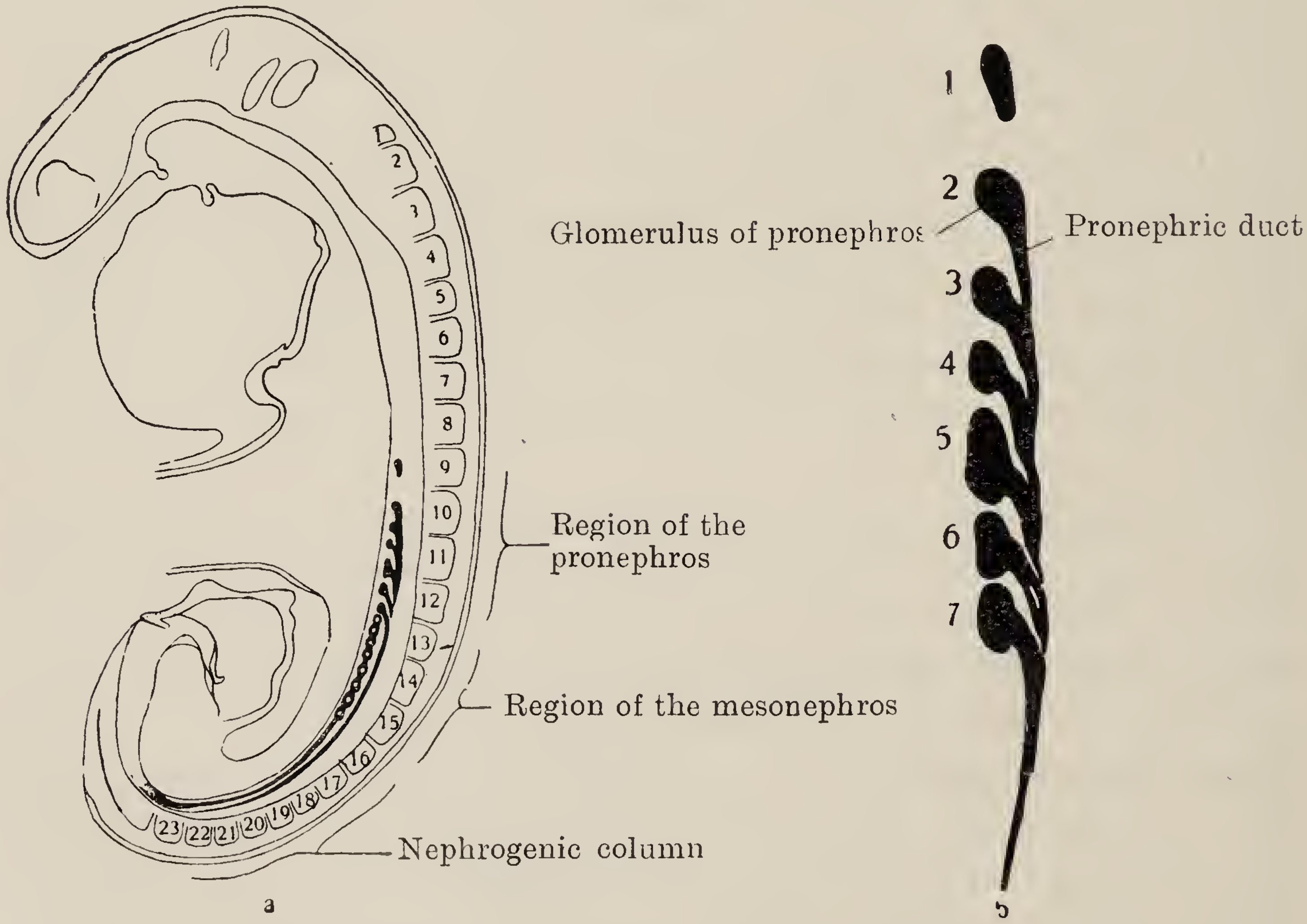

FIG. 8.—(*a*) Pronephros, mesonephros and metanephros of man in their segmental primordia. (*b*) The primordia of the pronephros of (*a*), in greater magnification. From Felix, development of the bladder and genital organs of man in the textbook of Keibel and Mall, Leipzig, 1910.

motor root of the spinal nerves. Their number, 31 in man, besides two rudimentary coccygeal nerves, total 33, thus gives the number of the myotomes.

Absence of nerves or myotomes occurs (e.g., in the region of the semi-spinalis dorsi et cervicis in man and in the tail musculature of many mammals), so that several myotomes are then innervated by one nerve (so-called "collateral innervation," Schumacher). But these variations due to phenomena of growth do not upset the above principle.

With regard to the nerve roots we therefore have to determine not only the myomerism but also the neuromerism. In the central organ enclosing the motor cells of these roots neuromerism is obliterated by the fact that in the body, at a later stage, we have to deal not with myotomes but with muscles, owing their existence to a fusing of myotomes, so that the segmentally arranged ganglia unite to form nerve nuclei for the muscles. Every motor root thus innervates a segment but only parts of muscles; numerous roots innervate the same muscle and it is impossible in the anterior column of the spinal cord to define segmentally the nerve-cells corresponding to separate segments even if we can distinguish by experiment and clinical observation the nerve cells of a segment. In fact it is not even possible to find the boundary of the segment externally on the spinal cord because the root fibres, particularly the sensory ones, leave the cord in bundles and intertwine with one another even before entering the nerve root.

On the other hand we have a true neuromere in the extension of the cord where the origin of the cranial nerves takes place from one segment each. Whether the encephalomerism extends to the mid- and front brain, as is often stated, is not certain because the significance of the small folds noticed in these parts of the brain has not been demonstrated (artificial products). The folding in the medulla oblongata alone may be regarded as the undoubted expression of a segmental division (fig. 7).

Thus neuromerism, at any rate in the spinal cord, is something secondary resulting from myomerism. On the other hand we find true segmentation in the nephrotome which originates in the mesoderm (fig. 8).

The horizontal division of the somite results in the formation of a middle portion situated between the myotome and the lateral plates, and this, therefore, encloses a dorsal recess of the body cavity. The vertical division separating the somites dorsally from one another extends to this portion, too, so that we get separate segments which are called nephrotomes, because portions of the excretory apparatus are formed from them. Just as the segmentation of the mesoderm is absent in the caudal area, segmentation of the nephrotomes is also absent, and so we have a cord known as the nephrogenic cord. From the nephrotomes and the nephrogenic cord, segmentally arranged, small canals arise: the pronephric, the mesonephric and metanephric canals. (In man the pronephric comes from the seventh cervical to the sixth thoracic segment, the mesonephros from the seventh cervical to the third lumbar segment, and the metanephros caudal to this, Felix). It is only with the

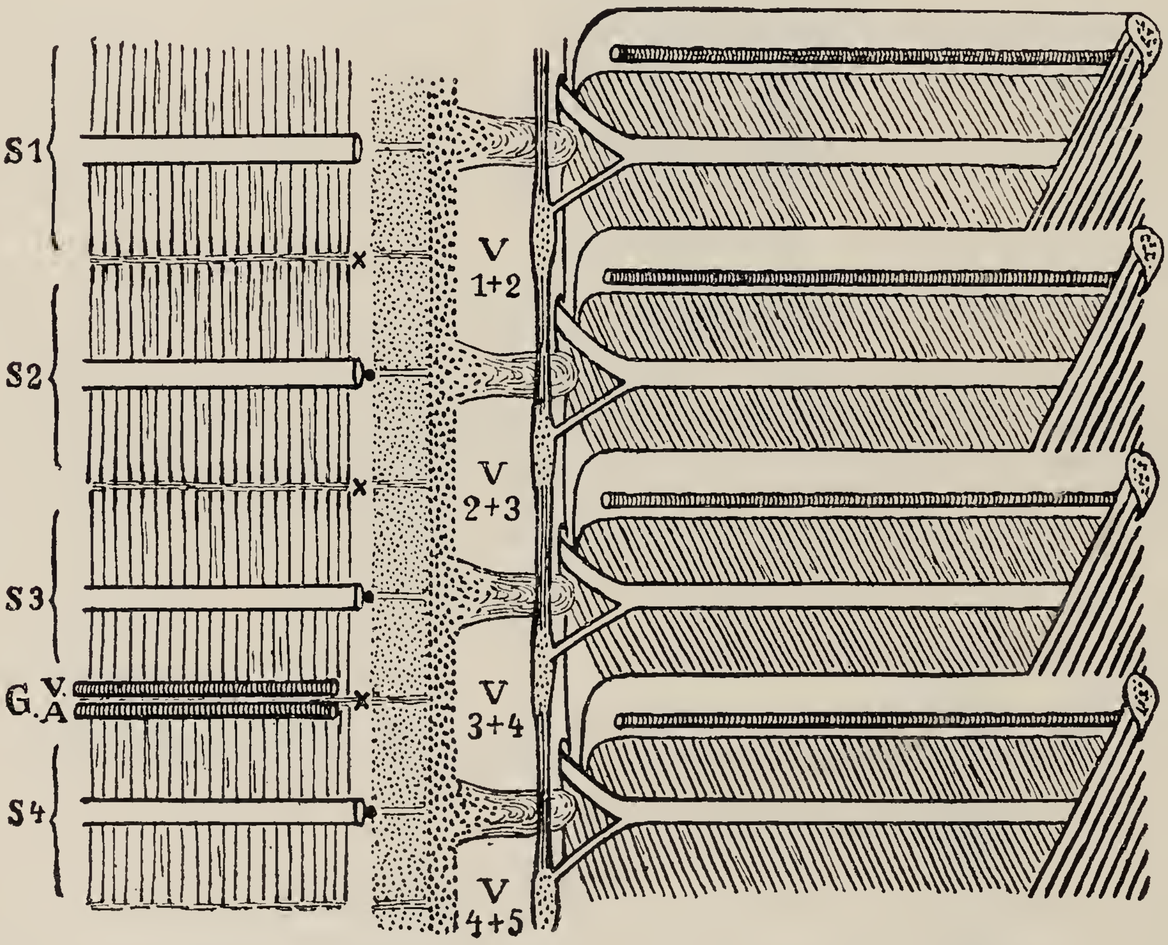

Fig. 9.—Scheme of the primitive and the persistent segmentation. On the left four primitive segments (S_1 to S_4). At (×) the intersegmental cleft with intermuscular connective tissue. The blood-vessels G. (A.V.) running in the intersegmental space. The finely dotted areas represent the primordia of the vertebral bodies with the intervertebral spaces which correspond to the middle of the myotome. The nerves (clear tubes) run from the intervertebral space into the middle of the myotome (●). Coarsely dotted areas represent the notochord with swellings at the level of the intervertebral spaces (nucleus pulposus) and annuli fibrosi of the intervertebral discs. On the right is a representation of an intercostal space. Explanation in the text.

pronephros that the primordium is purely segmented; with the other primordia additional canals appear later in every segment. The pronephric duct, too, since it arises by a fusion of the blind canal ends, is a segmental product, at any rate in its anterior portion.

If we reflect that the mesonephros is preserved, at any rate partially, in the testis, and the pronephric duct with its most anterior segmental opening survives as the ostium abdominale of the Fallopian tube, we see metamerism exercising a deep influence on the organization of the body.

In the higher vertebrates the segmentation of the mesoderm does not extend further ventrally, for the body cavity in such animals is invariably an undivided single space. But from the mesoderm comes the mesenchyme and the organs of the vascular and skeletal system produced therefrom. In these metamerism is pronounced.

The axial skeleton lies around the notochord in the form of skeletal-forming tissue projecting from the medio-ventral corner of the myotome (sclerotome). The primordia of the vertebral bodies send out the osteogenic membrane which embraces the neural tube dorsally, and from this the vertebral arch and its appendages arise. The whole becomes cartilaginous, and we have a series of segmentally arranged skeletal parts. But here the important fact appears (fig. 9) that the boundaries of the primordium of the vertebræ and the myotome are mutually displaced in such a way that a vertebral body and intervertebral disc at the middle of the myotome correspond to each myoseptum. This depends on the fact that every vertebral body grows together from two parts, each of which extends as far as the middle of the neighbouring myotome. Each vertebra thus belongs according to its ordinal number to two myotomes, and the whole intervertebral topography is explained by this. The foramen intervertebrale belongs to the anterior part of the sclerotome, and thus becomes the posterior part of the persisting vertebra. Behind the posterior portion of the foramen intervertebrale (not shown in fig. 9) comes the intervertebral cleft in which the intervertebral disc becomes involved with the remnant of the notochord. This point thus lies exactly adjacent to the middle of the myotome, so that the spinal nerve can enter the appropriate myotome immediately in an outward direction. On the other hand, the intervertebral vessels lie at first between two myotomes in the myoseptum on the cranial side of the nerves. The ribs similarly lie in the myoseptum on the cranial side of the vessels which already belong to the nearest segment, whereas the rib forms the caudal termination of the previous segment. Thus we get the arrangement of parts familiar to us from topographical anatomy, craniocaudally, rib, vessels, nerves (shown on the right in fig. 9, with the direction of the intercostal muscles and the segmental boundaries).

This situation is preserved very conservatively in the first and second myotomes (Bolk). The first metamere undergoes a progressive assimilation to the head. The dermatome of this segment, so far as it has not passed over into the ventral musculature of the neck, is situated entirely between the os occipitale and the atlas; (Mm. rectus cap. lat. and rect. cap. ant., rect. cap. minor and obl. sup.). This position thus completely agrees with the above scheme (fig. 9). A movement of muscle material along the axis of skeleton, such as occurs everywhere else, does not take place in the first myotome

(Bolk, p. 527). The M. rect. cap. major is innervated by N. cerv. 1 and N. cerv. 2, chiefly by 2.

What has been said above explains the fact that we have seven cervical vertebræ, but eight cervical myotomes and eight cervical spinal nerves and that the eighth cervical nerve issues in front of the eighth vertebra (first thoracic vertebra, behind the seventh cervical vertebra), the first thoracic nerve, first lumbar nerve, first sacral nerve, behind the first thoracic lumbar and sacral vertebra. The first coccygeal nerve issues behind the first coccygeal vertebra; but we have four additional vertebræ without myotomes and two rudimentary coccygeal nerves, so that the numbers of myotomes, nerves and vertebræ do not agree.

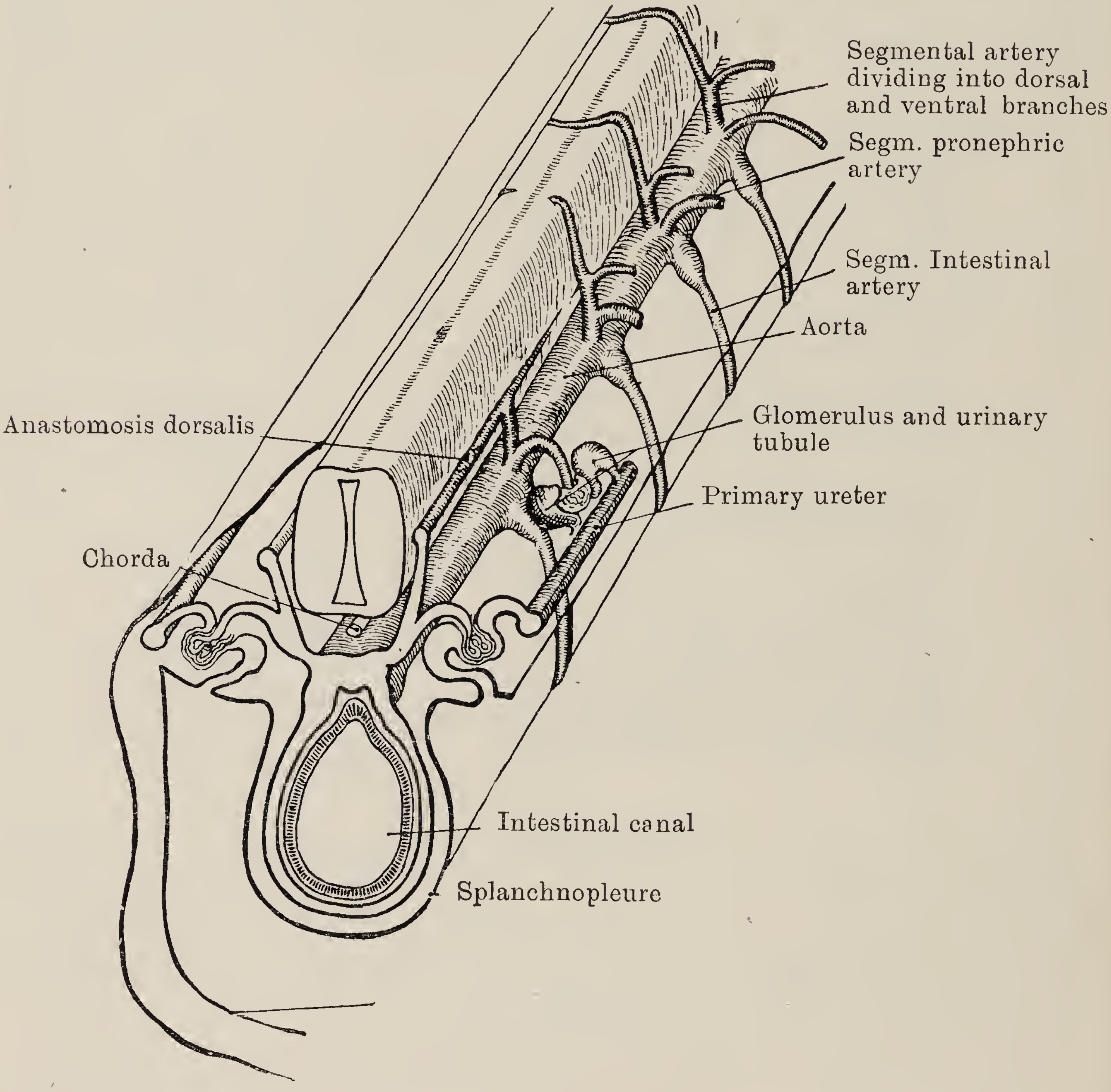

Fig. 10.—Schematic reconstruction of the vascular segments. (Borrowed from a figure in Keibel and Mall.)

This explains, for instance, the origin of the M. psoas, which arises in the main from the intervertebral discs. As to the ribs, these are associated with each vertebral primordium, but are developed, as a rule, only from the eighth to the nineteenth vertebra as independent bones, while in the remaining segments they are usually united with the vertebræ [cf. para. 56]. The alternating arrangement of vertebra and myotome, which is of such importance for the formal understanding of the body, has undoubtedly a mechanical value too, since, as may be easily seen, we get an effect on the vertebral column above all when one myotome acts on two vertebræ. The intervertebral area is then the point of movement.

The vessels, like the skeleton, are products of the mesenchyme. A division of the aorta into separate segments can even be demonstrated from time to time in the development of the vertebrate body. A vascular segment with definite division then corresponds to each segment of the body.

In each segment (fig. 10) there are three pairs of segmental arteries which can be called the parietal, intestinal and nephrotomic pair. The parietal pair belongs to the body wall. It arises between two myotomes, lies in the myoseptum, and divides like the nerves into a dorsal and a ventral branch. The dorsal branches in the surviving segments supply the dorsal musculature with the neighbouring parts of the skeleton and the skin covering them. The ventral branches of the parietal pair lie at first in the myoseptum. They can be recognized easily and clearly in the intercostal and lumbar arteries. In the cervical region they arise from a longitudinal stem, becoming a rudiment of the dorsal aorta and unite to form, by anastomosis, a vessel running longitudinally, the vertebral artery (figs. 30, 31). In the sacral region the lateral sacral artery plays a similar part as a longitudinal vessel. Longitudinal trunks, such as the internal mammary, the superior and inferior epigastric, are formed ventrally between segmental vessels also.

With the intestinal pairs, however, things are very different. These fuse at a very early stage into unpaired trunks, which again unite to form a few larger vessels. In the region of the fore-gut we find them as the bronchial and the œsophageal arteries issuing from the thoracic aorta ventrally. The lowest portion of the alimentary canal and the remnant of the fore-gut, as well as the whole of the mid-gut and hind-gut, are served by the three large vessels described in textbooks as unpaired branches of the aorta; the cœliac artery supplies the remnant of the fore-gut, the liver and the pancreas arising from the fore-gut, and the spleen. The superior mesenteric artery serves the umbilical loop (small intestine), ascending colon, transverse colon, and the inferior mesenteric serves the descending colon and the rectum. The nephrotome arteries necessarily remain in pairs. One of them is at first present for each mesonephric segment on each side (fig. 10). But as the mesonophros disappears, surviving partially in the testes, the definitive branches are easily recognized again as the spermatic arteries (ovarian artery), renal artery, and suprarenal artery. They form a part of the so-called "paired branches" of the abdominal aorta of the textbooks.

One very important and extensive area in which metamerism is seen still remains to be mentioned; this is an area connected with the distribution of the sensory branches of the spinal nerves. We know that a spinal ganglion corresponds to each segment, and that this ganglion lies in the foramen intervertebrale, or in other words, in the region of the myotome. The sensory nerves, too, conform to the division of the body into a dorsal and a ventral area (fig. 12). The direction of the cutaneous nerves, and their position enables us to distinguish an area thus supplied as a skin segment or dermatomes. The boundaries of the skin segments can be distinguished by following the course of the nerves of the skin; this direction depends on the position of their starting points in the skeleton, the growth of the musculature and the growth of the skin (Grosser), and this not only at the later embryonal periods, but as early as the time of the development of the germinal disc.

We find the nerves of the skin arising from the rami posteriori in the back running in a caudal direction very steeply downwards; the antero-lateral branches of the intercostal nerves marked by a course ascending in a cranial direction, and the antero-medial skin branches of the same nerves running in a caudal direction. These facts lead us to the circumstances which cause the nerves to take these directions. One such circumstance, for instance, is the growth of the M. trapezius (Grosser, Frohlich), which carries the nerves in a caudal direction with it. In the thoracic and abdominal wall the result is that areas of cutaneous innervation do not coincide with the intercostal spaces, but lie caudally from them. It has been proved by experiments that every nerve possesses a skin segment, i.e., a limited area. These dermal segments surround the trunk like a girdle, and here we have the important rule that every dermal segment overlaps the next in such a way that segment one covers segment two to the extent of one-third of its width, segment two overlaps one-third of segment three and so on. The sensibility of each point of the skin thus depends on several (three) sensory nerves.

The trunk has on either side a boundary line (Voigt) dividing the dorsal from the ventral dermal segmental area. This line starts at the back of the head, runs approximately to the acromion and then curves, concave externally, downwards as far as the gluteal region. The area of the back so defined is continued on the back of the head and on the extensor surface of the extremities. Its extent corresponds to the cutaneous branches of the posterior rami of the spinal nerves, which give us an insight by means of their course, ascending in a cranial direction and then distally downwards and outwards to the bony pelvis, into the displacements of the cutaneous areas, especially under the influence of the growth of the pelvis. The same applies to the anterior region corresponding to the anterior rami of the spinal nerves. We know that each of these rami possesses a lateral and an anterior branch, leaving the intercostal space. Here the skin areas are defined by a line which begins roughly in the sulcus deltopectoralis and then runs practically along the lateral edge of the rectus muscle. Each lateral branch gives off a twig directed posteriorly until it meets the branch from the dorsal division of the spinal nerve, and one directed forwards towards the middle line. We thus get a peculiar line of dehiscence, explainable only from the growth of the skin, running continuously through the skin from the region of the external auditory meatus to the second rib, thence as far as the iliac crest and so around the medial edge of the gluteal margin to the perineum. In the neck we observe the course of the cranial nerves like rays from the posterior border of the sternomastoid and in the lower region a similar ray centre at the margin of the gluteus maximus (perineal nerves internally, posterior scrotal nerves above, femoral cutaneous [small sciatic] nerve below). In the trunk this line of divergence of the cutaneous nerves is very plain in good preparations. It is a striking fact that this line of divergence of the nerve areas is the line of divergence of the hair streams.

The number of the individual skin segments is greater on the back than in the region of the anterior branches, because the anterior extremity withdraws five and the posterior eight skin segments from the skin of the trunk and utilizes them for the skin of the extremities (fig. 33). The seventh and eighth dorsal skin segmental areas (the last two cervical areas), and the twenty-fourth and twenty-fifth areas (those of the last two lumbar nerves) do not develop. If we disregard the four skin segments belonging to the neck we have twelve ventral and twenty-three dorsal cutaneous segmental areas belonging to the trunk. Here it is important to know that the last two cutaneous segmental areas forming the caudal portion of the trunk are a union of dorsal and ventral, while the perineum belongs to the ventral and the sacral region to the dorsal divisions.

Finally, we must think of the sympathetic nervous system, in the development of which segmentation is clearly visible. From each spinal ganglion a sympathetic ganglion develops (according to older notions; modern writers throw doubt on this method of development). The connection of the individual sympathetic ganglia by means of nerve fibres produces the sympathetic chain. This is most clearly seen below the neck in the trunk region, where there is a sympathetic ganglion to each segment, while in the cervical region the ganglion masses belonging to the eight segments form two or three ganglia. Generally there are only four sacral ganglia and often only four lumbar ganglia. Further, the first thoracic ganglion may fuse with the inferior cervical (stellate ganglion), so that the total number of sympathetic ganglia amounts to twenty-three—twenty-five up to thirty-one segments.

In a peripheral direction the grey rami communicantes run strictly segmentally with the spinal nerves to the skin, so that the boundaries of the cutaneous segments can be experimentally fixed by the arrangement of secretory and pilomotor nerves. The ganglia are, however, penetrated by sympathetic elements, for the intestinal nerves, too, heart and lungs being dependent on the eighth cervical and upper thoracic segments, rectum, genitals and bladder upon the upper three lumbar segments, stomach and gut, with the liver, pancreas and kidneys on the lower thoracic segments. It is remarkable that within the spinal cord the sympathetic nuclei are confined within the sixteen segments named above, eighth cervical to the third lumbar.

Para. 53. If we review all the known data with regard to the metamerism of the body, we see that it is possible to look at the body from the standpoint of segmental anatomy which forms the third branch of anatomy side by side with systematic and topographical anatomy. Segmental anatomy disintegrates like systematic anatomy, inasmuch as it describes parts outside their systematic relations, and constructs, like topographical anatomy, by bringing together all the formations belonging to like segments.

Let us take the third cervical segment as an example. To this belong the ~~posterior~~ part of the second and the anterior part of the third cervical vertebra, the second intervertebral foramen and intervertebral disc, a part of the diaphragm, and those parts of the deep cervical muscles which come from the vertebræ just named (Mm. longi, scaleni) as well as portions of the long muscles of the back, then parts of the trapezius and sternomastoid (anastomosis between the third cervical nerve and accessory), and the whole of the omohyoid and parts of the sternohyoid and thyreohyoid (ansa hypoglossi). Of the vessels a small part of the vertebral and its spinal branches must be included. We must add the anterior ramus of the third cervical leading to the cervical plexus, the posterior ramus of the same nerve and the grey matter of the spinal cord, further a portion of the superior cervical ganglion and the grey ramus leading to the third nerve with the corresponding area of the skin, glands, the muscles of the hair bulbs, and a portion of the pharyngeal plexus. To the skin area we must add a portion of the occipital region of the head (lesser occipital nerve), the entire cervical region as far as the clavicle and the shoulder (great auricular nerve, cutaneous colli, supraclavicular) and a strip of the skin of the neck (posterior rami) corresponding roughly to the sixth cervical vertebra together with the hair and glands of this sensory zone.

In the same way the body may be divided now segment by segment; to deal with the internal organs including the kidney, we require an exact knowledge of the vessels and nerves supplying them in the embryo; here embryology is of service to us. Pictures and models of all the parts belonging to the same segment, though they have only been provided in an incomplete form hitherto (van Rynbek), are possible and full of promise of good result. But the greatest value of segmental anatomy is the information it gives us as to the fate of metameric material. It is only in this way that we gain an insight into the changes of position suffered by the elements of the body which are at first so simply divided.

This change of position affects the muscles and nerves in particular. Thus in our example we see elements of the third myotome in the deep muscles of the neck, the lower muscles of the tongue, the long muscles of the back, in the diaphragm, and in the visceral muscles of the neck (trapezius and sternomastoid). The segmental nerves, after coming into close relation with the myotomes at their differentiation, have to follow all these changes of position. This they could not do if they continued their initially isolated courses. Thus the cervical plexus is the result of these displacements. Only dorsally where the myotomes remain in a state of greater rest do the nerves remain isolated (rami posteriores). A similar statement may be made as to the skin, the vessels, and the internal organs.

A knowledge of the segmental anatomy of man which is at present unfortunately hardly noticed in courses of instruction is of great value to clinical medicine (nervous diseases). This value is increased by the means supplied by segmental anatomy to assist us in comparing the form of the human body with that of other animals, inasmuch as the third segment, for instance, in man occurs in like position in all other vertebrates (cf. p. 99, allomerous homology). For example, we can thus determine that the muscles equivalent to those of the diaphragm are situated in non-mammals in the cervical region, and that in mammals they invariably proceed from like muscle material. We know from this that the ostium abdominale tubæ is the first pronephric opening and that the muscular axillary arch, observed as a variation, is no part of the pectoralis major, however closely connected with it. When formally equivalent formations develop from different segmental areas (e.g., the extremities, pelvis, etc.), then we are presented with a scientific problem which is only apparently solved by an assumption of "movement." The question is whether such movement [para. 75] is actually a displacement completing itself stage by stage in the descendants of a form or whether these forms which show, for instance, a different disposition of the pelvic girdle at different sacral vertebræ, are offshoots from series starting at different initial points and running nearly parallel to one another. The question is connected with the one concerned with strict monophyletic or polyphyletic origin. A solution is impossible at the moment.

Para. 54. And yet the metamerism of the human body does not by any means possess the high degree of development which is either conceivable or possible. More primitive animal forms have a much more highly developed metamerism, a fact which is important for us to know, because it leads to the question of the true inwardness of this remarkable mode of division.

It is true that we have to be careful (Grosser) not to regard many features of both mammals and non-mammals as "true metamerism." The bony girdles of the armadillo, the scales of reptiles and fishes, the pigment stripes of the horse and the cat, are phenomena which undoubtedly have nothing to do with metamerism because they do not agree numerically with either the number of myotomes or vertebræ. In part they may be connected with the movements of the body (scales), in part their character is still obscure (pigment stripes, Krieg).

On the other hand the more deeply we penetrate into this question the clearer does the proof become that the metamerism of man reproduces mere faint outlines of a picture more clearly defined elsewhere. Thus the metamerism of the muscles of the wall of the trunk in the acraniates, cyclostomes, fishes, and even of amphibians, extends to the ventral wall as well, whereas in higher animals and in man only traces of this are left (intercostal muscles, inscriptiones tendineæ of the rectus, see above). In the mesonephros possessed by all anamniotes, except amphioxus and the myxinoids, as a permanent urinary organ, the metamerism is more easily seen than in the kidney of the amniotes. Above all in two organ-systems, which in man and the higher vertebrates show nothing or only a trace, metamerism is found, viz., the cœlom and the gonads. In amphioxus and in many invertebrates the cœlom is originally separated into distinct chambers by partitions (fig. 11) and in each chamber there is the primordium of a gonad (Boveri, Zarnik) which arises in the somatopleure of the cœlom. It enlarges and penetrates the dorso-mesial wall of the preceding cœlomic segment, pushing forward the parietal epithelium of the latter as a visceral layer.

These conditions are clearly connected with those found in the Annelidæ, where segmentation is clearly confined to the mesoderm, and above all apply to the kidneys, the sexual organs and body cavity.

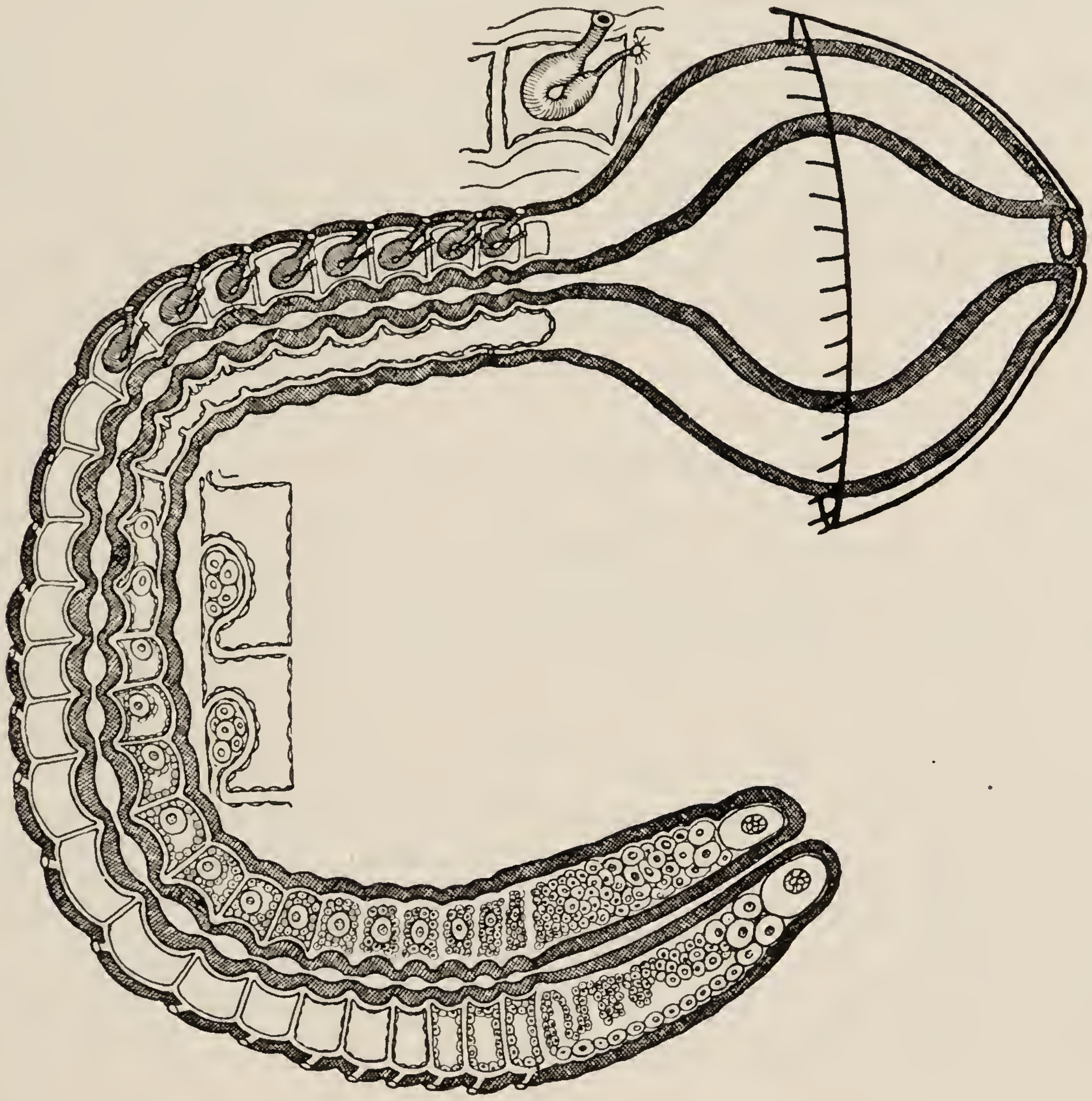

Fig. 11.—Longitudinal section through an annelid, Nais, drawn from a specimen of the Zoological Institute. The nephridia drawn from a specimen of *Lumbricus* of the Zoological Institute. The representation of the segmented cœlom on the left in the general body form of Nais was obtained from an illustration of Salenksky (Polygordius); the nephridia are reconstructed (cf. small frame on the left.) On the right the cœlom is represented in accordance with gonocœle theory. In the middle segments (small figure on the right), the picture of Zarnik's on the development of the reproductive organs of amphioxus is used.

Fig. 11 shows the mesoderm stretching in the form of a solid cord from the posterior end of the body to the front and divided into separate groups of cells in such a way that the oldest segment lies furthest towards the front while those behind attach themselves distally. In the cell groups a cavity appears (gonocyst, gonocœle) and the sexual cells appear in the lining of this cavity. Each segment is further connected with the surface of the body by a small segmental canal (kidney canal).

Here the question of the real character of segmentation arises What is the meaning of this transverse division of important organs which dominates the animal body, and of the repetition in polar arrangement of the elements of these systems which together form a segment? Not only the vertebrates but also arthropods and annelids owe their names to the obvious evidence of segmentation.

More than a hundred years ago the succession of a series of completely equivalent parts had led to the idea that their origin must be connected with a process similar in nature to sprouting Segmented animals were looked on as animal stems and the single segments as zoomites (Dugas in van Rynbek). The head was taken to be the starting point. There is in fact one kind of segmentation which conforms to this view to a certain extent, viz., that of tapeworms. But even in this case we do not have a true sprouting, since that would mean that every segment would have a head end and a tail end. In no case do these segments therefore possess the value of individuals, they are no more than body elements repeated by a budding process. The segmentation of the cestodes stands apart and cannot be compared with that of other forms because in annelids, arthropods and vertebrates the sprouting proceeds from the rear, while in cestodes it begins at the front. In the cestodes the oldest segment is behind, the youngest in front; in other forms the reverse is the case.

The attempt has also been made to derive metamerism from mechanical influences on the lines that the snake-like movements of animals had produced this mode of division. Like all Lamarkian explanations this leads into difficulties, because the object of transformation cannot be regarded as a cause [para. 19]. That a metamerism once begun may be assisted in its development by the movements of the body is conceivable.

But how does it come about? The fact that metamerism in the oldest animal forms, which show it, is confined to the mesoderm, and particularly affects the cœlom and the gonads, has suggested that metamerism is derived from the budding of sexual cells, and it has been supposed that the first point was their multiplication, the formation of sex individuals as opposed to the sterile head, a multiplication taking place from the back towards the front. Cavities appearing around each gonomere are supposed to have led to the formation of follicles which were further developed into segments of the cœlom (fig. 11, right). By assuming that the dividing partitions disappear we could understand the formation of the single cœlom, while the conditions in amphioxus would provide an intermediate stage.

According to this theory, founded by Meyer, and later supported by Rabl, metamerism is a division of the animal body, limited in the first place to the mesoderm, extending at an early stage to all derivatives of this germ layer (musculature, urinary organs, cœlom, gonads, axial tissue), and only secondarily reaching inwards and outwards, perhaps under the influence of locomotion, to derivatives of the entoderm and ectoderm.

This secondary segmentation occurs in limbed animals where, however, internal metamerism, and particularly that of the gonads, no longer survives.

In the vertebrates, including man, the secondary segmentation of the ectoderm (neuromeres, dermatomes) has been added to the primary stage, while that of the entoderm is only indicated to a limited extent by the course of the segmental nerves and vessels, while within the mesoderm the segmentation of the body cavity and of the gonads is no longer found.

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(2) Divisions of the Human Body

Para. 55. One of the most striking observations which the anatomist can make in regard to the divisions of the body is that the external division into head, neck, trunk and limbs is not an internal division, that there are no internal boundaries corresponding to these external ones.

In the region of the junction of the head and neck, the pharynx, the base of the tongue, and the salivary glands extend from one region to the other. Where the neck and trunk join, the lungs extend into the region of the neck. The boundary between thorax and abdomen cannot be drawn exactly (liver, spleen, alimentary canal and stomach in the thoracic region, pleural cavities in the renal area). The musculature of the extremities extends far over the trunk. Further, the cranial nerves cover a wide area in the neck and even penetrate into the trunk (vagus). Conversely we have the aortic arches of the head and neck ascending from the trunk, so that the neck, though in part only apparently, possesses no vessels of its own comparable to the segmental arteries of the trunk. In contrast with the highly differentiated state of the ventral area of the body is the strikingly simple formation of the dorsal region, while in man no caudal appendage is visible externally as a general rule, though rudiments of it can be demonstrated in his organization.

The phenomena just mentioned receive their explanation in the fact that our body is not formed by the addition of part to part, but is a unit in which subdivision occurs from secondary processes. It might be said that the vertebrate in its simplest form is a mere trunk-tail animal (acraniate); at a higher stage it is formed as a head-trunk-tail animal (cyclostome); then it becomes (fishes) head-trunk-tail-extremity animal, and at the highest stage it is a head-neck-trunk-tail-extremity animal. All these elements proceed from the trunk by transformations of single areas, tranformations which do not create new organs but change existing ones, alter their positions and thus bring them into new relations. If we can recognize and define a structural plan for the trunk what has been said above may be differently expressed as follows: head, neck, tail, and extremities contain no component which is not also present in the structural plan of the trunk. Our task is, therefore, to describe the structure of the trunk and its transformations.

(A) The Morphology of the Trunk and Tail.

Para. 56. We have already spoken of the polarity and segmentation of the trunk. The division into units produces a series of similar segments throughout the trunk. The axis of the trunk is traversed by the notochord (figs. 12a and 12b). Around the notochord lies the cartilaginous vertebral body from which springs an arch enclosing the spinal cord dorsally. Where the arches join dorsally the spinous process arises; from the arch at its origin from the body arises the transverse process (the posterior tubercle of the transverse process of the cervical vertebræ, the accessory process of the lumbar vertebræ).

The ribs (not shown in the figs. 12a and 12b), originally in unbroken continuity with the vertebræ, are separated from them and establish with the vertebræ a double articulation—ventrally with the body (the capitulum costæ), dorsally with the arch (tuberculum costæ). This holds for all vertebrates. Ribs are retained only in that portion of the trunk which becomes the thorax. Above and below the ribs retrogress, though represented in the cervical and lumbar regions. In the cervical region the ribs are represented by the anterior tubercles of the transverse processes, and in the lumbar region by what is commonly called the transverse process (costa lateralis). The common term, transverse process, is wrong; that this is so is shown by those cases in which it actually forms a rib (in the first lumbar vertebra for instance), or where the twelfth rib is reduced to a transverse process and the vertebra assumes a lumbar form.

Extension of the thorax and proportionate diminution of the cervica land lumbar regions occurs in a wide range of terrestrial vertebrates. Also in man we often find more or less than twelve ribs (cervical and lumbar ribs). In the sacral region the vertebral bodies, as well as the arches and rib rudiments (lateral masses) fuse to a single bone (os sacrum).

The retention of the ribs in the thoracic region depends not only on internal formative processes, about which we know little, but also on (Gegenbauer) the presence of the fore-limbs which, with the shoulder-girdle and its muscles, are attached to the ribs; in a similar manner the complete fusion of the sacral vertebræ and ribs depends on the attachment of the posterior extremity, particularly of the pelvic girdle; the girdle is articulated with the ribs (the lateral masses of the sacrum.)

A sacrum is present already in the amphibia in the form of a

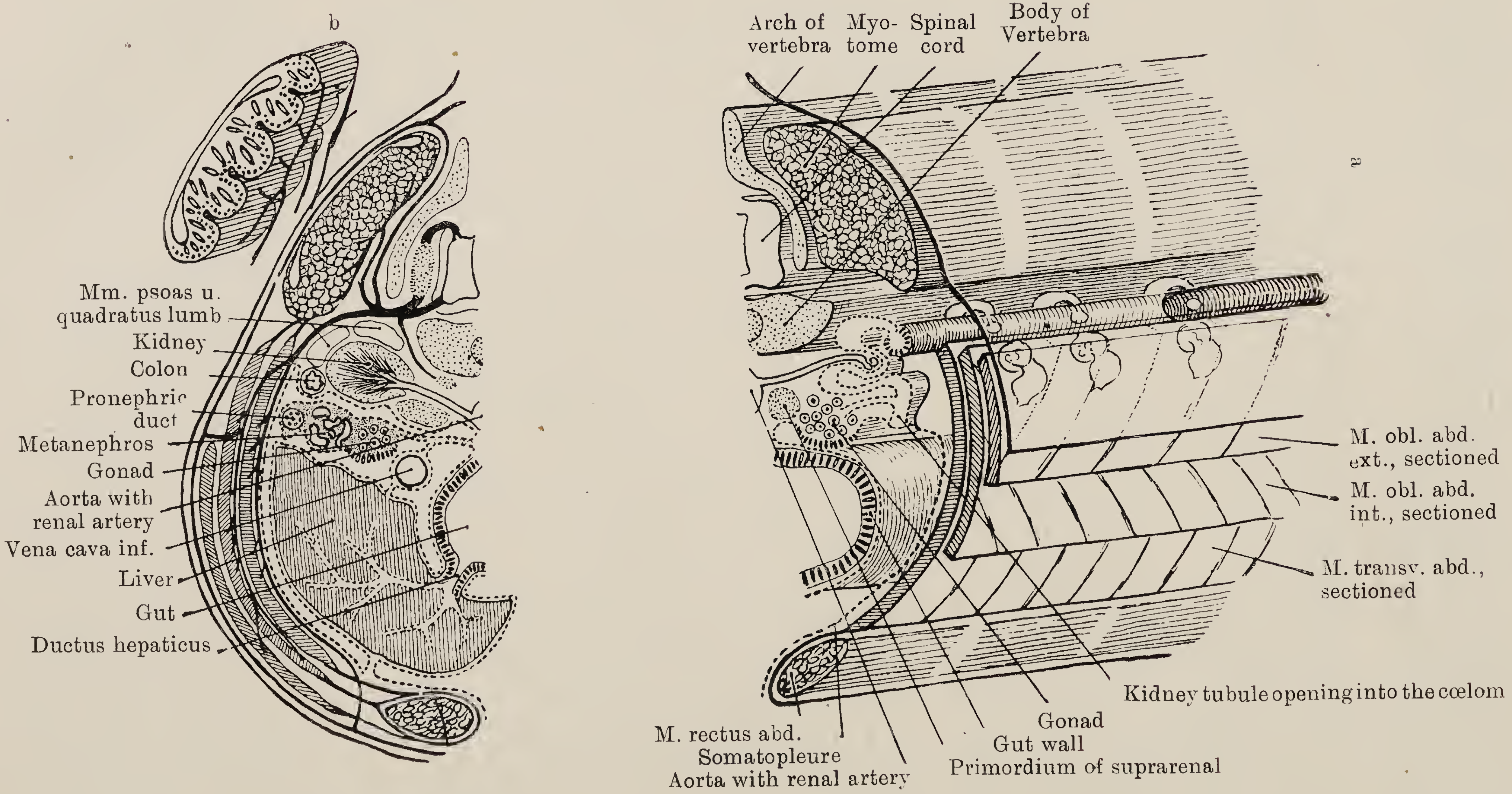

FIG. 12.—Schematic transverse section of the trunk. Explanation in the text. The transverse section "a" is artificial in so far as the vertebral body no longer shows such a form at this advanced stage of development. On the left the fig. 12b is an accessory sketch which is explained on p. 337.

single bone joined to the pelvic girdle. Though there is in the creeping animals no striking distinction between the more free anterior extremity and the more weight-bearing posterior extremity, yet it must be observed that from the very commencement there is a difference in the part which the anterior and posterior extremities play in movement. The posterior extremity shoves the body forwards, the anterior draws the body after it; participation of the trunk and tail does not yet allow the traction of the extremities during movement to exert their full combined effect.

When ribs are present they lie in the intermuscular septa, that is they are intersegmental. The ribs divide the trunk segments into a dorsal and a ventral half, the effect of which is expressed most clearly in the arrangement of the striate musculature.

A part of the striate muscle lies dorsal to the ribs and a part ventral. These are (fig. 12a) derived from the original myotomes (fig. 12b). The muscle fibres which arise from the medial wall of the myotome at first pass only from one segment to the next (fig. 12a). Through further growth there arise later more superficial and longer fibres which stretch over many segments. The so-called long or deep musculature of the back in man is the result of this process. The ventral musculature arises in primitive vertebrates in relation with this dorsal rudiment, and from this myotomic material the muscle buds grow into the ventral body wall (Maurer).

In the sauropsida and the mammals this relationship has become confused so that the muscle-forming elements at an early stage in embryonic development separate from the myotomic material without being recognizable as such. However, true muscle buds have actually been demonstrated in man (Zechel), so that our own body, as in many other things, exhibits very primitive features.

In the lateral body wall the sheet derived from the myotomic mass develops into the ventral musculature and of course in two systems—an anterior medial system (rectus system) and a lateral (obliquus system) (figs. 12a and 12b). This system was also arranged segmentally in the beginning. The inscriptiones tendineæ of the rectus abdominis and the infrahyoid muscles, as also that which frequently arises from the extremity of the eleventh rib and penetrates the internal oblique, are remains of this arrangement. The arrangement of this musculature is most perfectly expressed in the abdominal wall.

The rectus muscle occupies a ventral position, the oblique a lateral position. Originally in terrestrial animals where the trunk contributes to the locomotion of the animal they are richly laminated (Maurer), but the direction of the fibres allows three layers to be recognized. In mammals and man they are arranged in three sheets whose fibre planes cross one another at such angles that they exert a more constricting effect on the abdominal wall. The outer muscle runs from behind and above, to in front and below (obliquus descendens=external oblique); the middle from behind and below, to above and in front (obliquus ascendens=internal oblique); the inner one runs transversely (the transversus abdominis). The same arrangement can be discerned in the thorax if we ignore peculiarities that complicate the homologies—for example, the external and internal intercostals and the transversus thoracis (this latter is markedly reduced and is only retained behind and adjacent to the sternum). The rectus system in many mammals and monkeys reaches much higher and extends further outwards so that it comes to lie under cover of the pectoralis major. In man only a small portion of the rectus lies under cover of the pectoralis major (the pars abdominalis of the rectus), whilst farther laterally tendinous strands between the costal cartilages indicate the position of remains of the rectus. In the neck the infrahyoid muscles indicate the rectus system and the scalene muscle the oblique system.

Para. 57. Through the arrangement of the skeleton, in part also through the ventral musculature, there arise in each segment two spaces which by fusion between adjacent segments form two tubes. The dorsal tube surrounds the spinal cord and the ventral the alimentary canal and its mesentery. The spinal canal, the canalis vertebralis, opens outwards through the intervertebral foramina. From each intervertebral foramen there issues a mixed spinal nerve which is distributed to the corresponding myotome. The mixed spinal nerve arises by a dorsal sensory and a ventral motor root. The former takes origin from the spinal ganglion, the latter from the ganglion cells of the anterior horn; besides, each anterior root carries medullated preganglionic sympathetic fibres. Beyond the intervertebral foramen each spinal nerve divides into a mixed dorsal branch which supplies the dorsal musculature and the dorsal dermatome and a ventral branch which supplies the ventral musculature and the ventral dermatome. The sympathetic preganglionic fibres run to the sympathetic ganglia, which are segmentally arranged. From these ganglia post-ganglionic non-medullated fibres rejoin the spinal nerves, in order to run segmentally with them to the periphery (vaso-motor nerves, erector pilæ and sweat gland nerves). The entire distribution of a segmental nerve is shown schematically in fig. 12b.

The ventral tube embraces the peritoneal cavity that lies between the somatopleure and the splanchnopleure. Later both layers give rise only to the epithelium of the serous membrane, not to the striate muscle as occurs in the dorsal region [para. 62]. The gut is formed only from entoderm and is suspended from the mid-dorsal line by the splanchnopleure. The dorsal mesentery persists throughout the whole length of the gut (figs. 13 to 16). In the region of the œsophagus (fig. 13) a dorsal mesentery is present. In this region, however, owing to the position of the descending aorta and the vena azygos major, the layers of this mesentery become widely separated and form really the posterior portion of the mediastinal pleura.

The chief element of the dorsal mesentery is a connective tissue (membrana mesenterii propria), containing blood-vessels, lymph vessels, lymph nodules, nerves and fat tissue and covered on both sides by the peritoneum. At the root of the mesentery the membrana mesenterii propria is connected not with the peritoneum but immediately with the retroperitoneal tissue, particularly with that which surrounds the aorta (Toldt, p. 13).

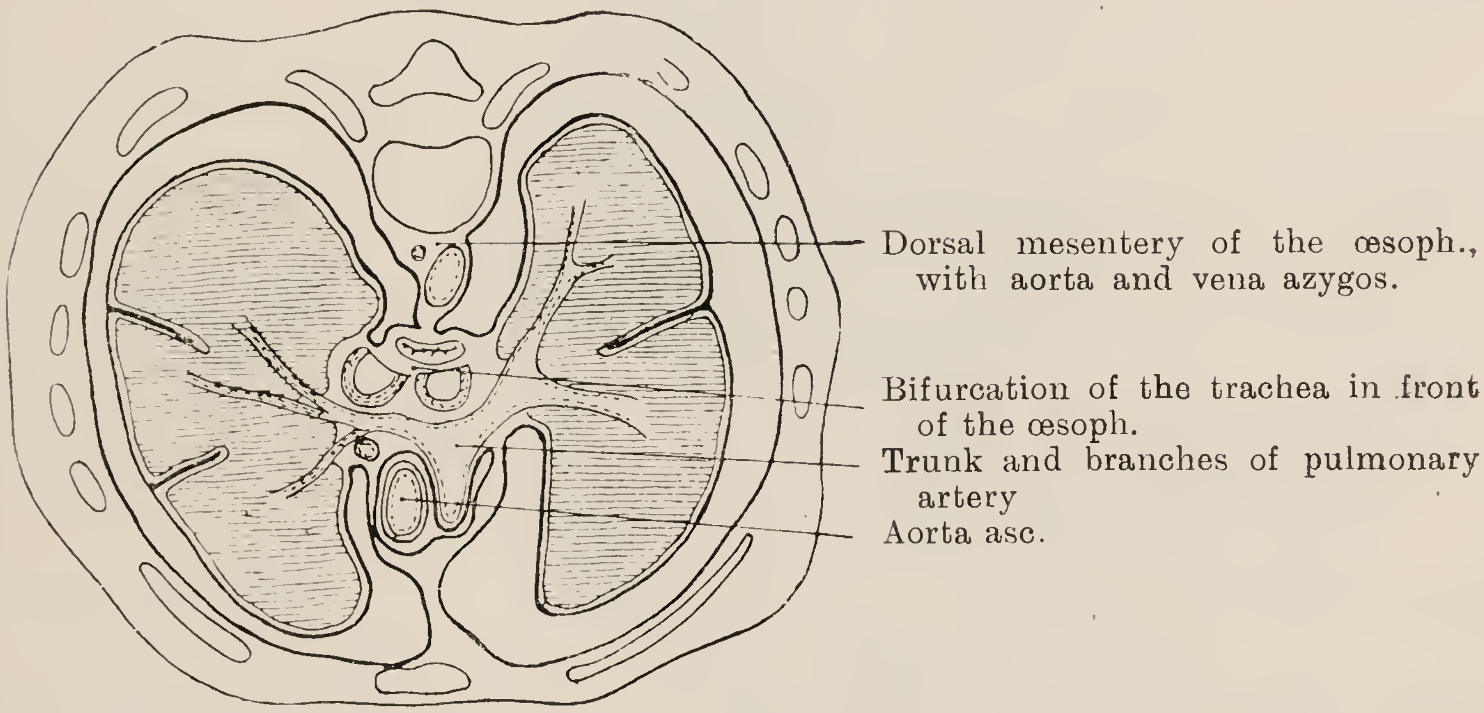
Dorsal mesentery of the œsoph., with aorta and vena azygos.
Bifurcation of the trachea in front of the œsoph.
Trunk and branches of pulmonary artery
Aorta asc.

FIG. 13.—Section through the thorax of an adult at the level of the bifurcation of the trachea. Adapted from Pratje, Anatomischer Anzeiger, Erg. Heft. 58, S. 96, fig. 6.

The ventral mesentery persists throughout the whole region of the fore-gut (figs. 13, 14, 15). In the region of the œsophagus it is continued as the anterior part of the mediastinal pleura forwards to the sternum. Behind the sternum it fuses into a thin, transparent double lamella. Between the œsophagus and the sternum the layers become widely separated by the pericardial cavity. This is shown in fig. 11 and schematically in fig. 14. When the pericardium is removed, the œsophagus is without a serous covering. Below the diaphragm, the ventral mesentery extends to the end of the fore-gut, that is to the point where the bile duct and the pancreatic duct open (pars superior duodeni). Through the interposition of the liver it is divided into a part between the liver and the stomach (lesser omentum together with the ligamentum hepato-duodenale) and a part between the liver and the abdominal wall (the ligamentum suspensorium). In this way the liver, the inferior vena cava passing behind it to the diaphragm, and the posterior abdominal wall remain without serous covering (fig. 15, vena cava inferior). Owing to the displacement of the stomach to the left and its rotation, so that its left surface becomes

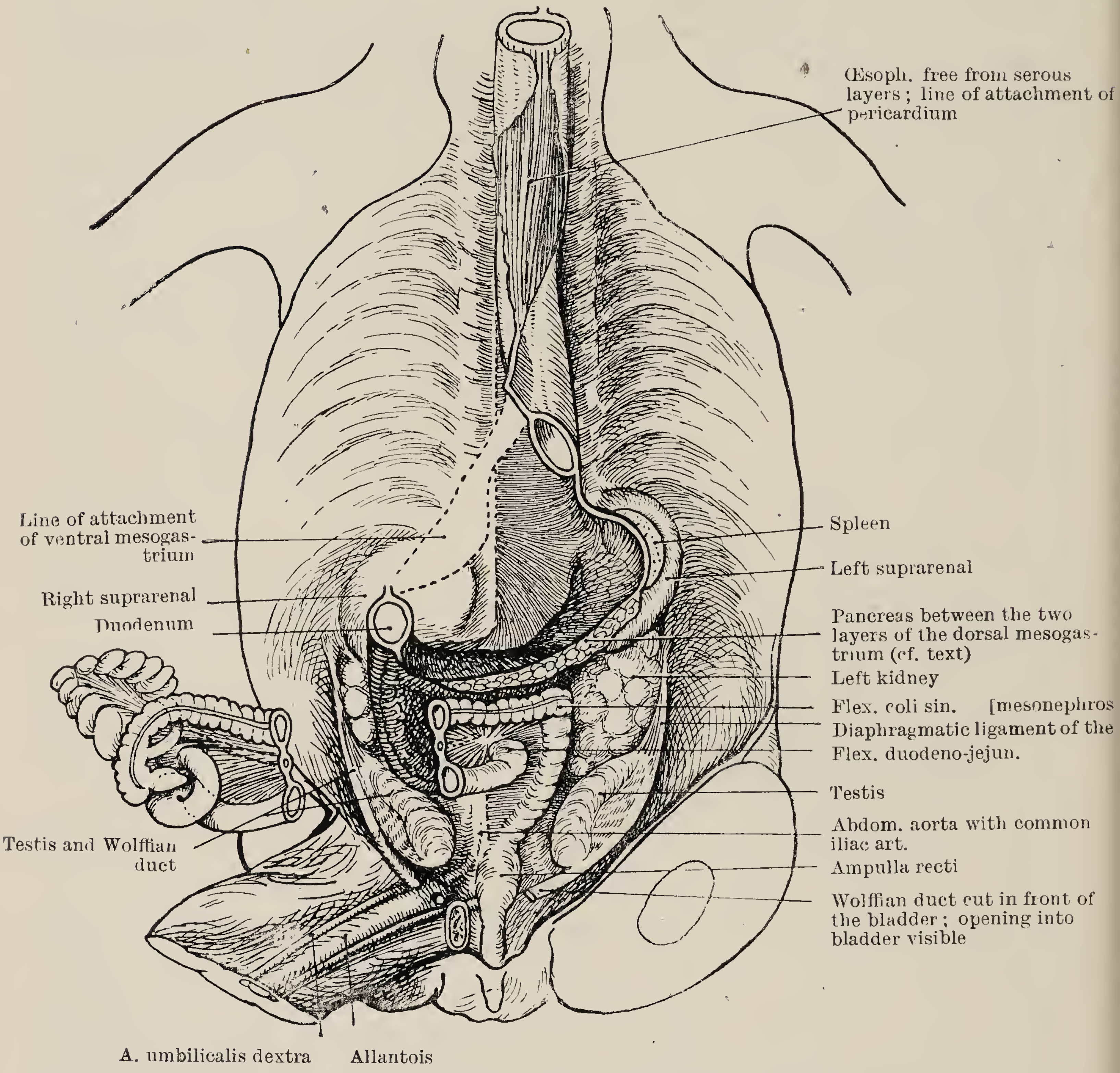
Œsoph. free from serous layers ; line of attachment of pericardium
Line of attachment of ventral mesogastrium
Spleen
Left suprarenal
Right suprarenal
Duodenum
Pancreas between the two layers of the dorsal mesogastrium (cf. text)
Left kidney
Flex. coli sin.
Diaphragmatic ligament of the [mesonephros
Flex. duodeno-jejun.
Testis
Testis and Wolffian duct
Abdom. aorta with common iliac art.
Ampulla recti
Wolffian duct cut in front of the bladder ; opening into bladder visible
A. umbilicalis dextra
Allantois

FIG. 14.—Scheme of the relations of the dorsal mesogastrium. The stomach is cut away just below the cardia and above the pylorus. The dorsal mesentery runs from the middle line (radiating lines) to the pancreas and spleen, surrounds these two organs and goes to the greater curvature. Before it reaches this it has been cut so that the pancreas is freely visible between the two layers. The ventral mesentery is indicated (fig. hepatogastrium and hepatoduodenale). View of the bursa omenti majoris. In the concavity of the duodenum the pancreas. The dorsal mesentery is here already degenerated. It reappears again in the form of the umbilical loop. In it the superior mesenteric artery. The umbilical sling with the coils of intestine lies in the physiological umbilical cavity. It is cut off near the origin of the umbilical cord. Based on a human embryo of 2 cm., crown-rump length. Drawn with a magnification of 1 : 15. Two-thirds reduced in reproduction.

anterior, there is formed between the liver and the stomach and the ventral mesentery on one side and the posterior abdominal wall on the other a recess, the so-called bursa omentalis, which naturally cannot overstep the middle line to the right since the dorsal mesentery starts from there (fig. 14). To the right of the middle line lies the caudate lobe of the liver (fig. 15), around which the vestibule of the lesser sac (also called the bursa omenti minoris) along with the recessus hepaticus extends. The dorsal mesogastrium is divided into two portions by the spleen, the gastrosplenic ligament and the phrenicolienal ligament (primitive). This latter, with the body of the pancreas included in it, becomes broadly attached to the posterior abdominal wall and so arises the secondary attachment of the dorsal mesogastrium, which runs from the diaphragm over the left kidney to the hilus of the spleen and then to the lower border of the pancreas towards the right. In the region of the small intestine the ventral mesentery is no longer found and the dorsal mesentery acquires new relations. The first portion of the gut is developed as an umbilical loop from the posterior abdominal wall; in consequence of this the dorsal mesentery acquires a curved attachment from which the loop is suspended (fig. 14). Out of the loop is developed the whole of the small intestine and the ascending and transverse colon. This mesentery,

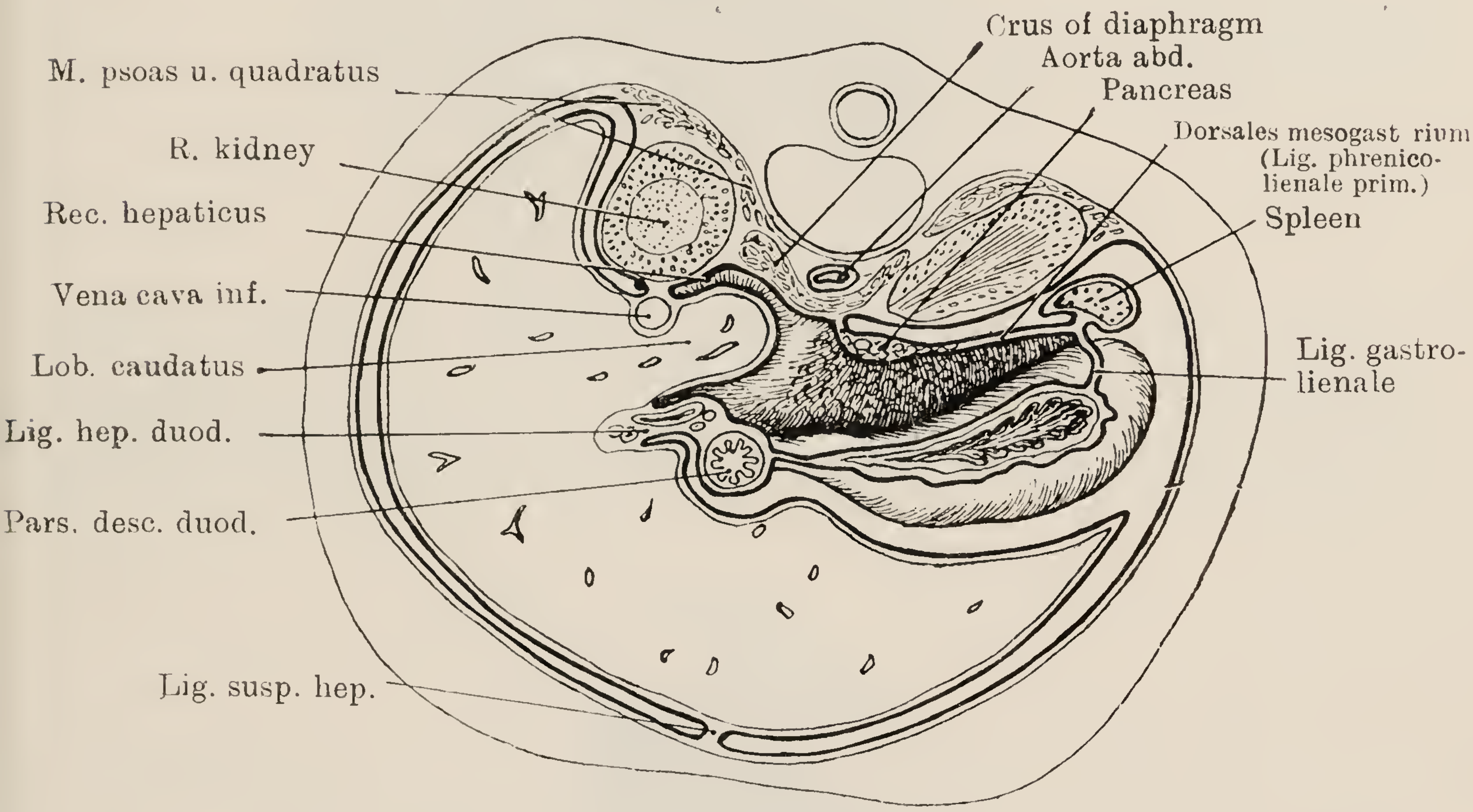

Fig. 15.—View of omental bursa from above. Explanation in the text. Based on a transverse section, 3 mm. thick, of a human embryo of 9 cm. crown-rump length. The under surface is at the level of the umbilicus. Enlargement 1 : 5. Two-thirds reduced in reproduction.

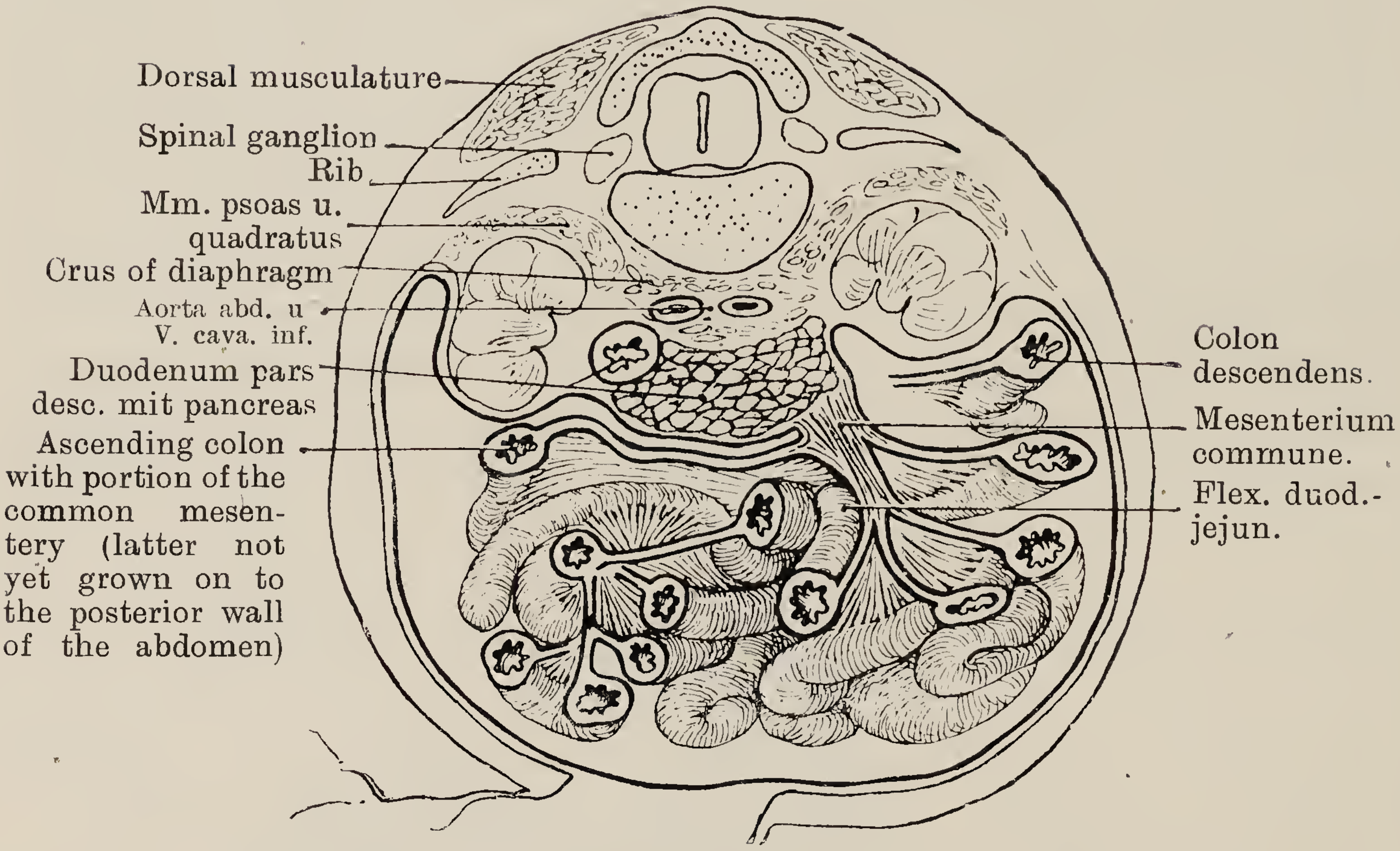
Dorsal musculature
Spinal ganglion
Rib
Mm. psoas u. quadratus
Crus of diaphragm
Aorta abd. u V. cava. inf.
Duodenum pars desc. mit pancreas
Ascending colon with portion of the common mesentery (latter not yet grown on to the posterior wall of the abdomen)
Colon descendens.
Mesenterium commune.
Flex. duod.-jejun.

Fig. 16.—The same embryo as fig. 15. The succeeding section enlarged 1 : 5, under surface at the level of the umbilicus. Three-quarters reduced in reproduction. On the left the descending colon with its mesocolon is schematic and drawn without relation to the general mesentery. The common mesentery has a small intestine part and a part attached to the ascending colon which has not yet disappeared on the posterior abdominal wall. If one imagines this to happen so the root of mesentery here disappears.

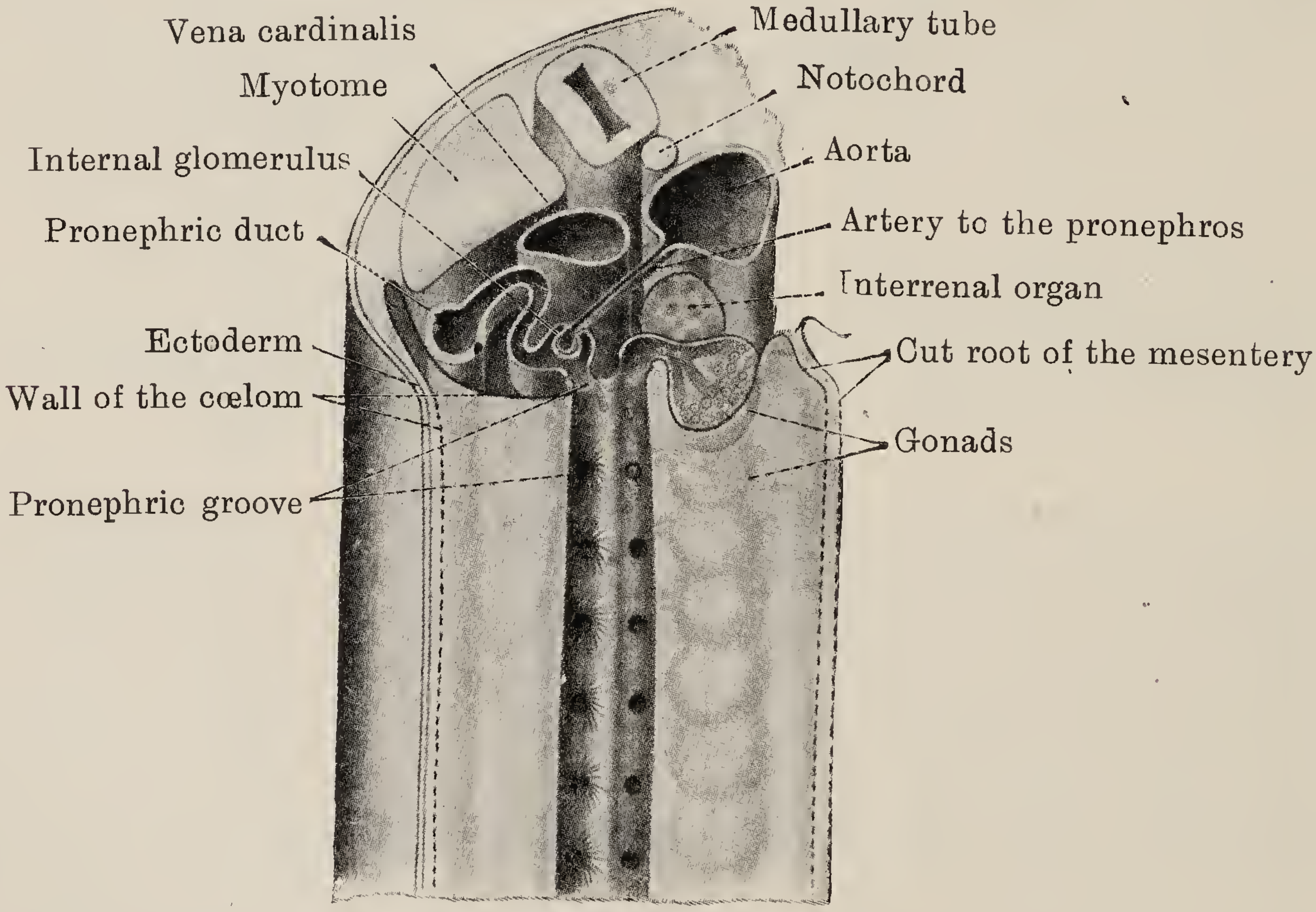

Fig. 17.—An attempt at a schematic representation of the formal value of the urogenital connections. Gonad and excretory apparatus opening by a single opening in the marginal renal ridge. The sexual products fall into the ridge and pass along the excretory channels. Excretory apparatus is in the pronephric stage. (From Lubosch, "Embryology of the Female Genital Organs" in the textbook of Halban-Seitz, fig. 48.)

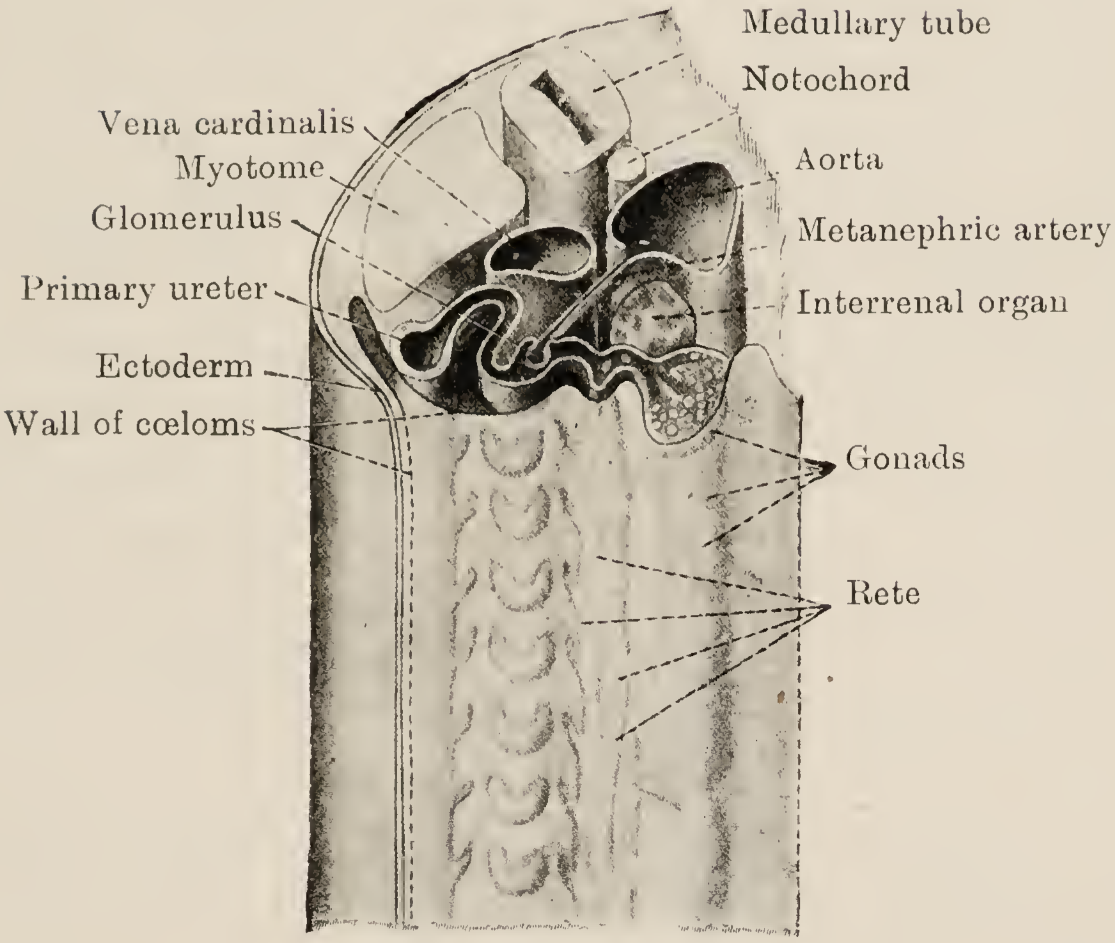

FIG. 18.—Excretory apparatus at the mesonephric stage. The kidney ridge has become transformed into a canal. In this the formation of divisions and anastomoses (original form of a rete, which stands in open connection with the gonads and Bowman's capsule). (From Lubosch in Halban-Seitz, fig. 49.)

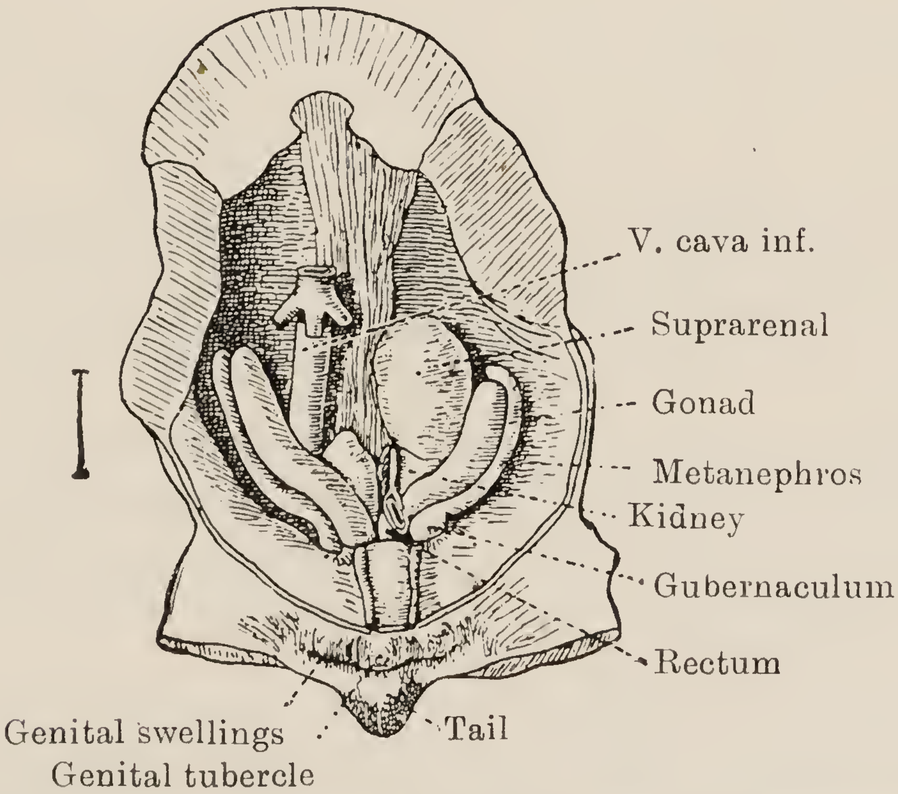

FIG. 19.—Dispositions of the sexual organs in a 13-mm. embryo. Enlargement 1 : 17. Specimen from the Marburg collection. (From Halban-Seitz, fig. 51.)

which forms a curved attachment for the umbilical loop, is called the common mesentery. Later this extends on the posterior abdominal wall and along the dorsal mesogastrium. In this way is established the root of the mesentery, the secondary attachment of the ascending colon and of the transverse colon to the under surface of the great omentum. Caudally the primitive attachment of the dorsal mesentery continues along the colon. From this position it fuses with the parietal peritoneum.

Before the secondary attachment of the cœlom takes place the wall of the body cavity possesses a primary peritoneal covering. This forms on each side the covering of the kidneys and between them the lower surface of the omentum majus. After completion of the process this lower surface of the omentum coalesces with the upper surface of the mesocolon transversum, the renal peritoneum on each side with the mesocolon and descendens. All three adhesions can always be separated in older embryos and children and often in adults, so that the primitive situs can be restored (Vogt). The primary peritoneum forms the anterior surface of the fascia-capsule of the kidney ; the kidney itself develops in the subperitoneal tissue which supplies the posterior leaf of this capsule.

Para. 58. Corresponding to the secretory function which the cœlom possesses in the early stages of development, the vertebrate body also possesses in the dorsal connections of the cœlom with the ancestral vertebrate cœlom an excretory system (figs. 10 and 12) which corresponds functionally to the nephridia of the invertebrate, even if it does not strictly correspond in a formal sense. This is demonstrated by the segmental canals of the pronephros and mesonephros. In fig. 12a the primitive connection of a canal of the mesonephros with the Wollfian duct is shown. The other end is joined with the cœlom. It has been suggested (Boveri) that this duct, in the ancestral vertebrate, might have been a groove in the ectoderm which joins these canals together in a segmental fashion (fig. 12, on the right).

The canal is connected with a vascular whorl (figs. 10, 12a, glomerulus), a segmental mesonephric branch derived from the aorta. In further development the connection of the canals with the cœlom is lost and it then forms the mesonephros, an elongated gland which is situated retroperitoneally.

Medial to the rudiment of the mesonephros the gonads and the interrenal bodies (= the cortical part of the suprarenal) develop. Both these organs in their further development are retroperitoneal. Between the Wollfian duct and the gonads segmental connections develop which later form the rete testis and the rete ovarii.

We assume for the understanding of this remarkable formation (Felix) that in more primitive forms it may have been a dorsal recess of the cœlomic cavity which has become transformed into a canal (marginal kidney canal, fig. 16). Such a longitudinal canal forms one type of ordinary duct in the urinary organs of the selachians. In the higher forms, owing to the retrogression of the mesonephros it is transformed into an excretory apparatus of the genital glands.

In the male, these canals become the true excretory ducts of the testis. In the female they acquire no sexual significance, being developed from the bisexual stage and of only vestigial account. The permanent kidney is developed from a more caudal part which corresponds to the excretory duct of the mesonephros. At the beginning the kidney is very small, and lies (as a pelvic organ) covered immediately by the suprarenal and the gonad. These, through the growth displacement of the organ primordia and the growth of the trunk, come to acquire their adult positions (figs. 19, 20, 14).

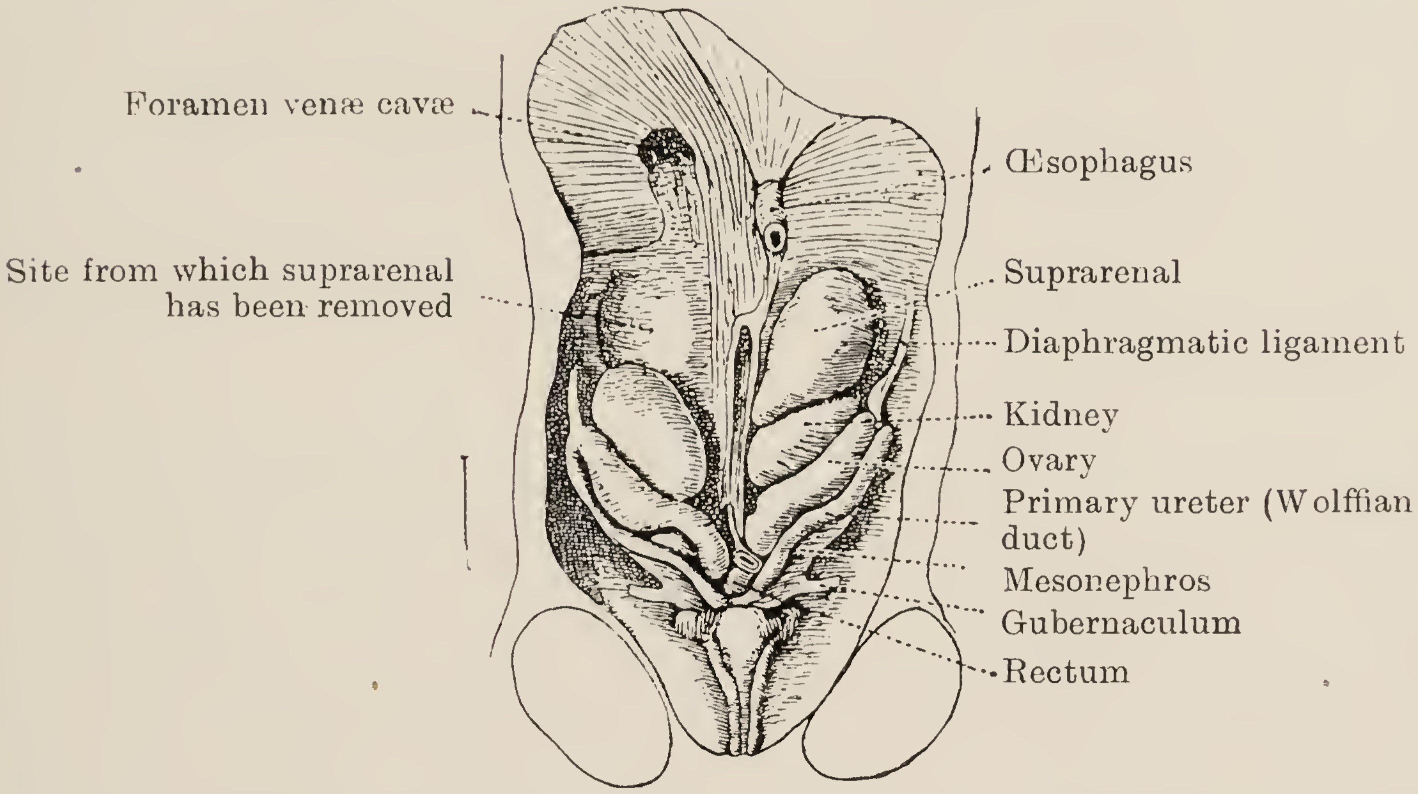

FIG. 20.—Disposition of the sexual organs of a 20-mm. long (crown-rump) female embryo. Enlargement 1 : 7. Specimen from the Marburg collection. Five-sevenths reduced in reproduction. (From Halban-Seitz, fig. 52.)

The arteries of the trunk come from the dorsal aorta which arises as a single tube from the aortic arches (cf. figs. 30, 31). They lie in consequence behind the gut and in front of the vertebral column. Their segmental branches have been previously mentioned [para. 52 and fig. 10].

The dorsal segmental arteries are the intercostals and the lumbars. The subclavian and the common iliacs are also segmental arteries in origin [para. 32], whilst the stem of the aorta is continued as the caudal artery. Only in man, owing to the size of the iliacs and the reduction of the middle sacral, does the aorta assume the appearance of dividing into two end arteries.

Para. 59. It thus becomes clear how great a difference there is between the dorsal and the ventral area of the body. The great complexity of the ventral half is in marked contrast to the uniformity of the dorsal half. The ventral differentiation that is caused by the limb buds, by the complication of the alimentary canal and the retroperitoneal organs, does not occur in the dorsal region. The uniformity of this area is summed up in the term "back." In unchanged form and without any variation its structure is continued forwards as the neck and backwards as the tail.

For the understanding of the latter the fact that it is only a continuation of the back is of importance. All the ventral parts are absent from the tail (gut, cœlom, kidney). On its ventral aspect there are muscular elements which are supplied by the ventral divisions of spinal nerves. In a typical tail segment there are to be found the notochord, caudal vertebræ, caudal part of the spinal cord, caudal nerves, caudal muscles, and the caudal aorta with dorsal segmental arteries.

It is not easy to determine a definite limit to the anterior extremity of the tail. If one were to describe as tail vertebræ all that lie behind the sacrum, even then this would not furnish a limit, since in various animals the same number of vertebræ may or may not be included in the sacrum. Thus, in man, where the normal number of vertebræ composing the sacrum are the 25th to the 29th inclusive, one often meets cases where the sacrum comprises 25 to 28; 24 to 28; 25 to 30; 26 to 30. The coccyx of man (normally vertebræ 30 to 34) does not correspond to that which comprises the free tail vertebræ of other animals since this includes vertebræ distal to 34 which are not present in man. The caudal region of man is therefore not of the same morphological value as in the tailed animals (not homologous). As tail muscles, the mammals possess a musculus extensor caudæ dorsalis, an abductor caudæ, and a depressor caudæ, the last two of ventral origin and supplied by ventral nerves.

In man, these structures are present, but in part are reduced, in part transformed for other purposes. It is only occasionally that an extensor caudæ can be clearly demonstrated on the coccyx. The abductor caudæ appears as the coccygeus and is reduced almost to fibrous tissue, and fuses with the sacro-spinous ligament. The depressor caudæ is represented by the levator ani. Both muscles, though topographically belonging to the perinæum, are not supplied by the pudic nerve, but by the sacral plexus. This demonstrates that these structures of the pelvic outlet are derived from elsewhere. For the occasional segmental caudal nerves which, in man, are reduced to two very fine twigs (the first and second coccygeal nerves), supply only the rudimentary extensor coccygeus and tail skin. They therefore contain only dorsal primary divisions (rami ano-coccygeus) with motor and sensory fibres for the parts mentioned.

This whole caudal region in man forms the so-called cauda interna (occulta). A cauda externa (libera) has been observed in man quite rarely.

The external human tail, which arises as a malformation in children, is not a true tail since it usually only presents a skin appendage without any internal differentiation. It is a true tail if segmental elements are demonstrable, such as chorda, myotome, neural tube, vertebræ. The most interesting are, of course, those which show an excess of vertebræ corresponding to the true caudal vertebræ. These, however, have not occurred in man. Six coccygeal vertebræ may be present, but these arise by anterior displacement of the sacrum, so that the total number of vertebræ is not increased. When vertebræ have been observed in the tail appendage they always appear as overgrown coccygeal vertebræ, the number remaining the same. On the contrary, tails with developed muscular and nervous structures have certainly been observed. All tail formations (true and untrue) are to be related to the animal tail which has preserved the developmental primordia for the tail parts.

The coccygeal hairiness, when it develops excessively, is to be compared with the hairiness of the area of attachment of the animal tail. Developmentally, the human embryo always possesses at an early period a true excess of vertebræ (36 to 37 instead of 34). It has therefore, indeed, not only an internal but a true external tail, with tail myotomes, dorsal segmental tail arteries, and the primordium of the tail gut itself. The typical "back" formation is not recognizable in the tail region.

(B) Morphology of the Head.

Para. 60. The consideration of the head brings us to the question referred to previously, how far is the typical structure of the body repeated in the head? This falls, as is obvious, into two subsidiary questions. Firstly, if in the head region a subdivision comparable to that of the trunk is present? Secondly, how do the essential constituents of which we recognize several (notochord, vertebra, myotome, lateral plate, cœlom, excretory organ, nerves, blood-vessel) repeat themselves in the head?

The first question is to be answered in this sense, that head segmentation comparable to the segmentation of the body does appear in part; it does not, however, affect the whole head and is joined with other differentiations which have segmental character but are not homologous with the segments of the trunk. The answer is more understandable if we put the question in another way, in how far does the head retain those elements which are comparable to the trunk? [general homology, para. 29]. Since the head possesses the entrances to the alimentary and respiratory tracts, and in addition also special sense organs, which are not present in the trunk, it follows that the head must develop a special form of its own. This anterior head form is influenced by the organs of smell and sight and further through the mouth and nose.

The special position of the smell and sight organs depends on their anatomy since they are derivatives of the brain itself. The olfactory nerve is composed of the fibres of ganglion cells lying peripherally. The bulbus oculi is to be regarded as a peripheral lobus opticus (brain wall = retina, ventricle = the cavity of the optic vesicle, later the space between the two layers of the retina; membranes = choroid and sclera; fibre path = the optic nerves; artery = ophthalmic artery from the cerebral artery, the internal carotid.)

The skeletal parts of the skull which enclose these sense organs are the olfactory capsule (ethmoid) and the orbit (the anterior part of the body of the sphenoid and the great and small wings). In the anterior part of the skull there are recognizable no elements corresponding to the vertebræ. On the contrary in the posterior part of the skull those elements which develop in cartilage suggest such vertebral elements. This is also suggested by the notochord which traverses the base of the skull. Its anterior end lies in the bottom of the sella turcica and indicates the boundary between the anterior and posterior parts of the skull, or, as it is better called, the evertebral and vertebral parts of the skull. This description is based on the fact that cartilage and later bony vertebral primordia develop beside the notochord and extend from it in the skull region. These primordia do not develop individual structures as in the trunk region, but fuse together to form one whole mass (parachordal bars, centres for the occipital and the posterior half of the sphenoid.)

In the fishes and many amphibians persisting during life, and in amniotes only during the embryonic stages, the gill arches and gill slits introduce a new element of specialization in the head region. This latter, in contradistinction to the somitic division, is peculiar to the head. It rests on the successive perforations of the pharynx by which, for respiration, water comes into contact with the gills.

Between two gill openings there lies a partition. The opening of the mouth is similarly surrounded on either side and below by a partition. All these gill arches contain skeletal parts, muscles, blood-vessels and nerves which are known as the visceral arches, muscles, vessels and nerves.

Since these visceral segments have nothing to do with the trunk segments, and the trunk segments do not occupy the vertebral region of the skull, so there remains the question if there develops in the head region any part of the same validity which it has in the trunk segmentation. We have seen above [para. 54] that the mesoderm has such features, above all in the trunk segmentation, and it is therefore necessary to consider the mesoderm of the head. Is this divided into myotome and lateral plate?

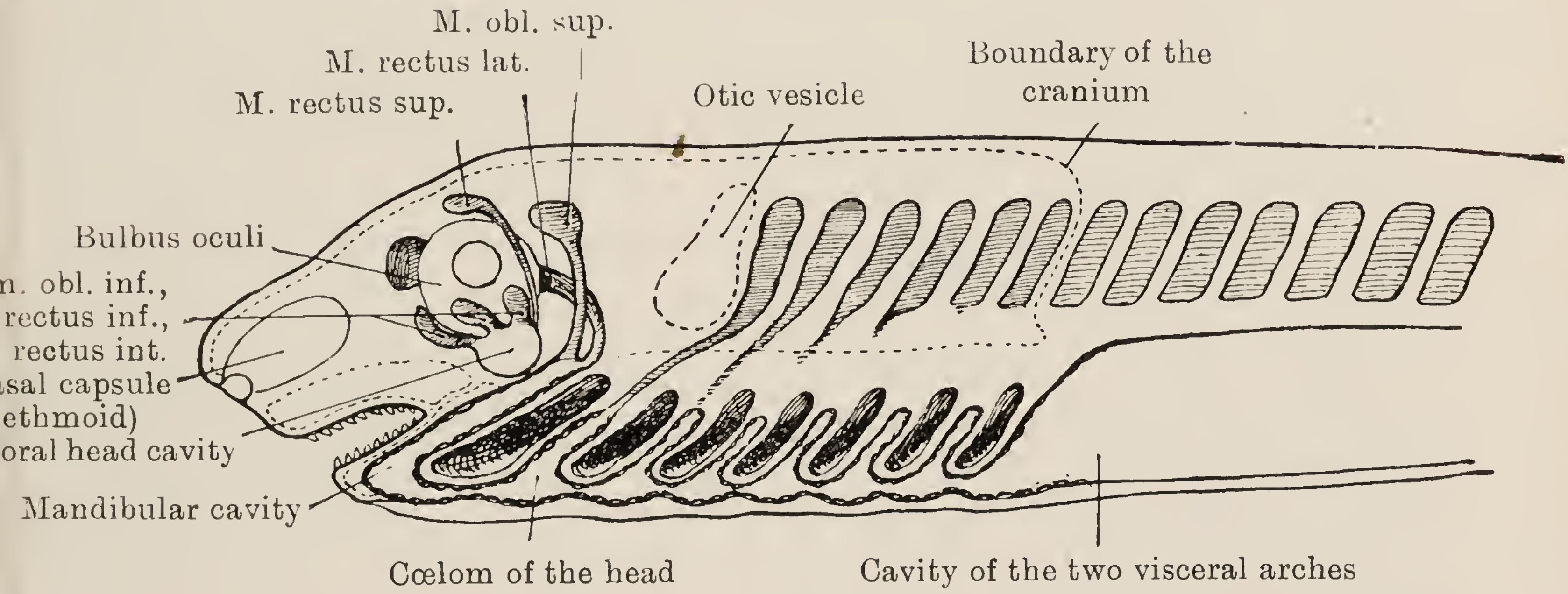

FIG. 21.—Scheme of the vertebrate head. Boundaries of the cranium and otic vesicle indicated by dotted lines. Pro-otic myotomes in relation to the pre-oral head cavity and mandibular cavity. Post-otic myotome in relation to the head cœlom; the latter in connection with the single trunk cœlom. The head cœlom divided by the gill slits.

Indications of such a division are present. Despite much difference of opinion yet this much is certain, the mesoderm lying in the dorsal region of the head is divided into myotomes and ventral segments which correspond to the lateral plates in the trunk region. In the head this lateral mesoderm is further divided since the gill arches penetrate it. The dorsal myotomes stand partly in relation with the lateral plates; certainly is this the case in the first two. In respect to the fate of the dorsal mesodermic myotomes it is certain that the eye muscles are developed from those portions of it that lie in front of the otic vesicle, whilst that part which lies behind the otic vesicle disappears without forming any muscle. [On the fate of the lateral plate see para. 52]. The total number of myotomes to be found in the embryo is uncertain. This uncertainty is partly due to the difficulties of observation and partly due to variation in embryos themselves. The myotomes of the head may arise in great numbers, may fuse together or disappear. The most certain number is in the selachian embryo where there are ten: four in front and six behind the otic vesicle.

We thus get a segmental division in the head though not in the skull. This division is indicated by the myotomes, the head cavities, and the visceral arches (branchiomery). What part the visceral arches play in the organization of vertebrates is not clear. The old idea that their relation to the skull is the same as that of the ribs to the vertebral column presents certain difficulties. And it has been rightly pointed out (Bütschli) that if the visceral arches were equivalent to the ribs the visceral clefts ought to be in the upper part of the myosepta. But they are not. The visceral arches, like the visceral clefts, probably represent something peculiar to the gill area.

Para. 61. Immediate conclusions as to the metameric division of the cranium itself cannot be drawn from what has been said above, but some conclusion may be come to, if regard is had to the cranial nerves (Gegenbaur). These nerves are undoubtedly in metameric order; at their exit points we have marks which can be immediately compared with one another.

The extent to which the exit of the cranial nerves is valid for homology depends on the constancy of their relation to the surrounding parts [paras. 27-29]. Furthermore, if one agrees that there is a spinal ganglion to each segment, then one can determine from the number of ganglia the number of skull segments. For this the number of ganglia must be known.

Comparison of the nerve exit-points show firstly, that the visceral arches innervated by the cranial nerves correspond to the (hypothetical) metameres of the head, and further, that we can determine the number of the segments which have united to form the vertebral skull from the number of the cranial nerves.

If we now compare individual skulls with regard to their extent, keeping the nerves in view, it appears that the cranio-vertebral boundary in vertebrates is not everywhere the same.

In all amniote skulls the hypoglossal nerve is the last cranial nerve, whereas in more primitive skulls the vagus is the last cranial nerve. Moreover, even this is not the most primitive arrangement. In the cyclostomes the skull includes the facial and the acoustic nerve, but the vagus arises behind the skull. This has been described as the palæocranium in contradistinction to all the others which are known as the neocranium. In the neocranium again, the older form in which only a few segments are added from the original trunk area is distinguished as the protometameric neocranium (selachians and amphibians) from the auximetameric cranium in which still further segments are added.

But now we must distinguish between the addition of trunk material to the head and vertebræ to the skull. The former takes place to a large extent and for the reason (Gegenbaur) that the autochthonic primitive vertebral material has largely disappeared. But the attachment of vertebræ to the skull occurs only in a small occipital area, and teaches us nothing about the hypothetical origin of the primitive cranium. This is for us a historically given magnitude. It probably originates in the union of a definite number of segmental vertebral primordia, just as the head has been produced by the union of a definite number of trunk metameres of acranians.

The theory of the palæocranium and the neocranium rests upon the idea that at various times attachment of trunk metameres to the skull have occurred; the boundary being thus pushed to the rear and the roots of trunk nerves becoming those of a cranial nerve (N. hypoglossus).

The basis on which this idea rests cannot here be extracted from the literature (Froriep, Fürbringer and Gaupp). As to the manner in which this addition came about and the mechanical and functional factors which brought it about, much, in fact all, is obscure. From the purely morphological point of view we must accept the fact, as we must in all like cases, that it has actually happened. How to explain it is another question, on the answer to which the fact does not depend. Probably the attachment of the skeleton of the gill arches to the trunk vertebræ plays a part. Also the attachment of the shoulder-girdle to the trunk vertebræ plays a part in the production of the protometameric cranium of the selachian (Veit). For the later additions there is no evidence at all as to what factors might have been operative. One must regard the growth of the skull as a special growth; for instance, the development of the occipital joint for extension of the head. Certainly none of the factors are known. An acceptance of an orthogenetic trend in development would under such conditions lead us only to the same obscurity.

The following three schemes present the essentials of the three types of skull. (See fig. 22.)

The object of human anatomy is to seek these basal phylogenetic principles and understand how they affect the structural plan of the human skull. This is naturally only possible in the cartilaginous cranium, since the ossification of the skull creates new relationships. In the primordial cranium we look for the boundary between the evertebral and vertebral part of the skull in the sella turcica where the notochord ends. The evertebral part forms the facial skeleton.

The olfactory capsule forms a nuclear area in which the cartilaginous ethmoid develops, and to this is added the anterior part of the body of the sphenoid and also the wings of this bone. (These latter are also partly included in the orbit.)

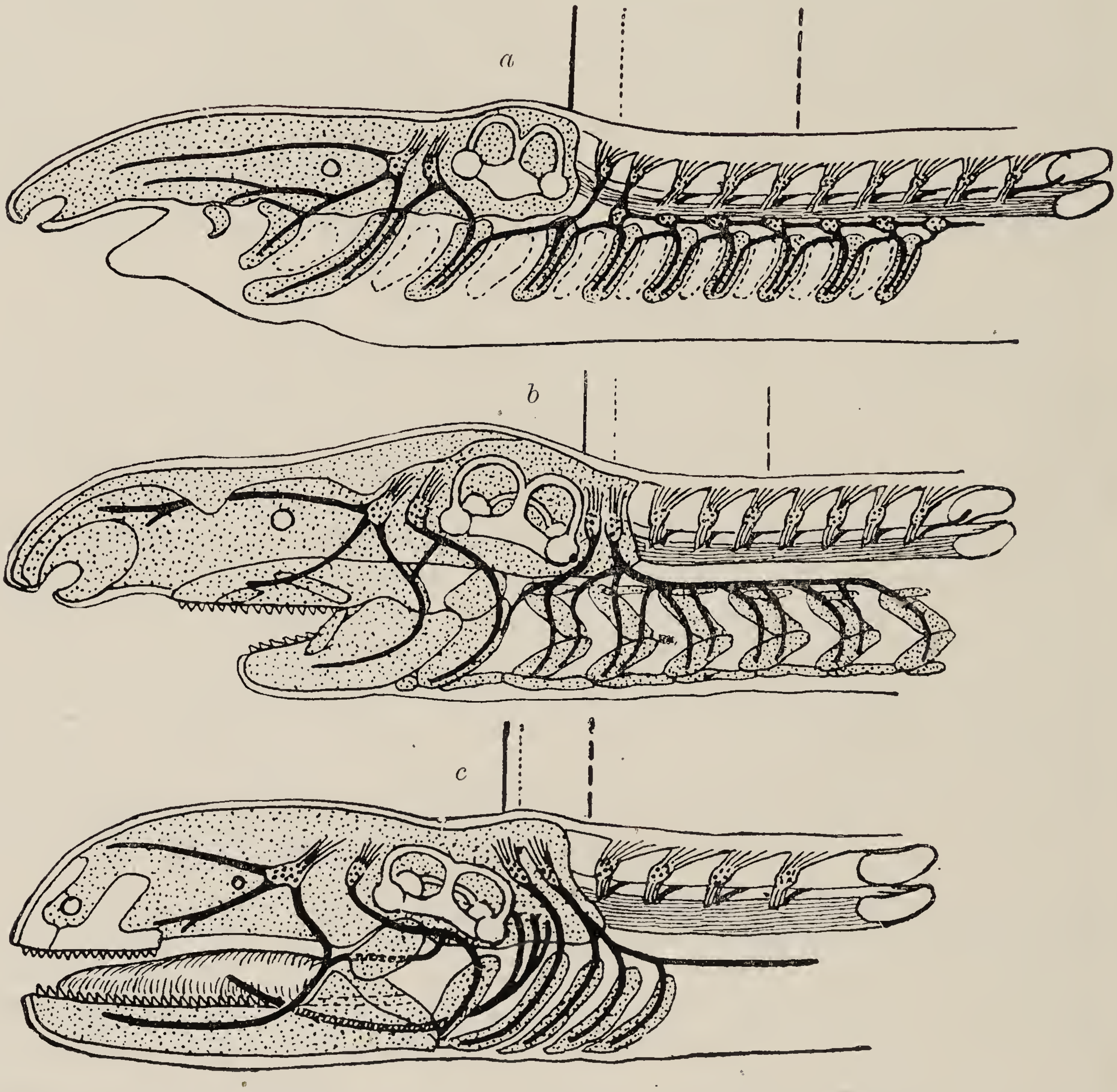

Fig. 22.—Three schemata for the elucidation of the formation of the head. Above palæocranium (based on the skeleton of the head of Petromyzon in Bütschli's "Introduction to Comparative Anatomy.") In the middle and the lower the neocranium, and of course in the middle the protometameric type (Amphibia), below the auximetameric type. The vertical lines indicate the displacement of the posterior boundary of the head backwards while the different posterior limits remain parallel to one another. In fig. *a* (the thicker line) lies behind the ear region, in *b* (finely dotted line) behind the vagus, in *c* (the broken line) behind the hypoglossal. In front of the ear lie the trigeminal and the facial. Behind the ear (in *b* and *c*) the glossopharyngeal and the vagus. In *a*, the glossopharyngeal is schematically represented as an independent nerve ; behind is the vagus in whose trunk seven ganglia are interspersed above the gill slits. One finds in *a*, *b*, *c*, the spinal cord lying above the notochord, with the spinal nerves arising by dorsal and ventral roots. The first three spinal roots in *b* form in *c* the hypoglossal (fig. *c*). Three thick black roots behind the ear.

In the nasal capsule two cartilaginous bones develop, the ethmoid and the inferior turbinate. The nasal, lachrymal and vomer arise as membranous ossifications superficial to the nasal capsule (facial bones in the nasal region). Situated ventral to them the mandible and the maxilla, both formed in membrane, are developed as parts of the facial skeleton.

The basal chorda dorsalis persists as the ligamentum apicis dentis between the vertebral column and the occipital bone. The cartilaginous parachordal bars in the basis of the skull form the body and lateral parts of the occipital and the posterior part of the body of the sphenoid. That portion of the occipital which lies above the medulla oblongata and there joins its two lateral parts together develops in cartilage. It is this part which resembles the neural arch of a vertebra and has been the starting point of the older vertebral theories of the skull (Goethe, Oken). The addition of a whole vertebral primordium, which is the consequence of the conditions already referred to, explains the similarity. Laterally lies the auditory capsule which forms the basis of the cartilaginous petrous temporal.

To this are added in the region of the vault of the skull membranous bones; frontal, parietal, squama of the temporal, the tympanic ring, the interparietal. These bones form together the vault of the skull enclosing the brain.

The mammalian skull, and, of course, the human skull, has besides these features, which it shares with the amniote skull in general, many peculiarities which develop hand in hand with the complexity of the brain. The vault of the skull to which reference has already been made grows further. Cavities which in reptiles and birds lie outside the skull become included in it in mammals. In general the dura mater in all amniotes includes a space of the same value, so that the exits of the cranial nerves afford a criterion of its extent, and in this way any increase in size can be estimated. The exit points from the dura mater are everywhere comparable (primary), whereas the exits from the bony parts of the skull are not so. (These are secondary [Gaupp]). Only in the glossopharyngeal, the vagus, and the accessory do both the meningeal and the bony exits correspond.

The difference is most marked in the case of the trigeminal. The whole course outside the dura, which the third, fourth and fifth nerves take, is not present in the reptiles and birds. The ganglion semilunare, like that of the ninth and tenth nerves, lies outside the skull. The cavernous sinus is an extracranial structure in the sauropsida. The facial canal is a peculiarity of the mammals, for in reptiles and birds the facial nerve leaves the skull at a higher point corresponding to the hiatus facialis.

In the non-mammals there is no bony connection between the capsule of the eye and the nasal capsule. The ethmoidal nerve (naso-ciliary) runs freely between the two capsules. In the mammals this extracranial region belongs to the anterior fossa of the skull. The nerve in mammals now describes a course from the orbit into the anterior fossa of the skull and then into the nasal cavity. The cranial cavity has been enlarged at the expense of parts that were originally extracranial (protocœlic and auxicœlic types of skull [Gaupp]).

The visceral elements are suspended ventrally from the cranium. These parts, described as visceral arches, are, in the beginning at any rate, cartilaginous. Each ossifies later in several typical portions. Only the first, the so-called Meckel's cartilage, is situated in the midst of membrane bone. The most massive part of this, the os dentale, bears the teeth, and in mammals and man is the chief element of the lower jaw. A second bony element is present in the non-mammals. This part in the mammals is no longer part of the lower jaw but forms the annulus tympanicus.

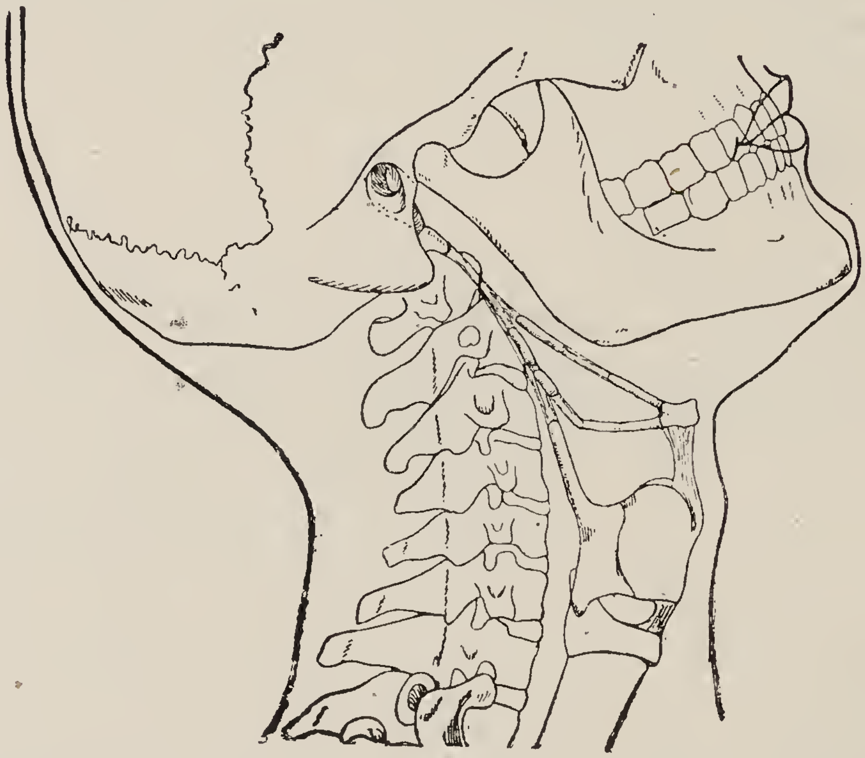

Fig. 23.—Fully retained 2, 3 and 4 gill arches in an adult. After v. Eggeling in Jenaische Zschr. f. Naturw. Bd. 53.

The arches are numbered and named thus: The first is the mandibular arch; the second is the hyoid arch. The rest are numbered as one to five from before backwards. They occupy an area extending from the skull to the trunk. The five gill arches, when they are complete, as in fishes, are divided into four parts (cf. figs. 22 and 26). The uppermost of these hangs from the skull, where it joins the vertebral column, whilst the lowest is joined by an unpaired piece, the copula, with the corresponding part of the opposite side. The copulæ together form a central unpaired sternal-like plate. The hyoid also was segmented in a similar manner. Its dorsal portion is clearly found in amphibia attached to the auditory capsule. It corresponds to the stapes of mammals. The next portion described in mammals and man as the hyoids reaches right to the copula. The first arch shows only two subdivisions—an upper (quadrate) and a lower portion (Meckel's cartilage). Between the two is situated the primary joint of the jaw in the non-mammals. In respect to their morphological significance the gill-arches are to be looked on as something secondary to the gill-slits, whose walls they form. During embryonic life the gill-slit appears as an internal and external depression which ultimately breaks through and forms a complete cleft. Both gill-arches and slits in the terrestrial animals undergo retrogression in part, and in part give rise to new organs and structures.

Man possesses four arches and five internal depressions which do not break through to the exterior. In addition, elements of the fifth, sixth and seventh persist without, however, forming arches. A clue to the fate of the seventh arch can only be derived from the developmental history of lower vertebrates (amphibia), and particularly in forms where it is well developed. The original and peculiar cartilage of the larynx of amphibia (cartilago lateralis) arises from the seventh visceral arch. From this special cartilage are derived the cricoid cartilage, the arytenoid cartilage and also the cartilaginous rings of the trachea and the bronchi. The connections of the seventh visceral arch, therefore, extend themselves as far as the lungs, which are derived from the fore-gut. From the sixth visceral arch develops the cartilage of the epiglottis and also the cuneiform cartilage lying in the arytenoid folds. The thyroid cartilage clearly arises in the most primitive mammals from two successive cartilages, the fourth and the fifth, joined by a copula. This origin is indicated in man by the foramen that is often present in the cartilage. The body of the hyoid represents the copula of the second and third visceral arches. The greater cornu arises from the third visceral arch, the styloid process and the stylohyoid ligament between the styloid process, and the lesser cornu from the second arch. In particular cases part or the whole of this system may be present, as, for example, an ossified stylohyoid ligament (v. Eggling [fig. 23]). From the first visceral arch develops Meckel's cartilage. Its cranial end forms the malleus. The joint between it and the uppermost portion of the arch is the malleus-incus joint, the uppermost portion being the incus itself (figs. 25 and 27).

The internal depressions in man give rise to a series of fossæ such as that for the tonsil and, above and below the level of the laryngeal nerves, the sinus pyriformis.

It is now quite clear from these homologies that the visceral arches are not limited to the "head" but stretch far into the trunk region where, as has already been seen, the gills function. From these remarkable facts the question arises how are we to assess this great extension backwards of the visceral arches? Two widely divergent theories have been put forward. One considers the gills of the craniotes as something quite sui generis, and believes the breaking through of the floor of the pharynx, with all its consequences, to arise out of the needs of the organism. The so-called branchimeres are not to be regarded as derived from something still further back in the history of the organism but are to be looked on as such, i.e., responses to the needs of the organism (Veit). The other theory goes right back to the numerous gills of the acraniates and, since these have no head, relates the gills to the anterior part of the trunk. They then become incorporated in the head formation in this region, influence especially the consolidation of the cranium and attain a new position. Here again there are two possibilities. Either the position of the visceral arches in the trunk region is the remains of the primary position or originally all the arches belonged to the head region and reached the trunk region by a shifting of their position, The latter is not improbable since the teeth-bearing function of the first arch carries it right up to the region of the auditory capsule. For the unfolding of the posterior arches only the trunk area is available. We leave this undecided but accept the view that the gills are an old possession of the acrania, for it has this advantage, that it can be shown with certainty that the fishes possess in front of the mandibular arch yet two more arches—in structure, of course, not recognizable as small arches, and in front of the mandibular cleft a pre-oral (premandibular) head cavity (pre-oral arch) (lip cartilage). These, if one looks at them from a functional ætiological point of view, may be said to have been sacrificed to the development of a similar mouth space. They are found also in the amphibia, and leave behind them, whenever they are present remnants in the muscles and nerves. Since it is difficult to believe that they can arise without any reason—so far as we know they are never functional—it proves rather the view that they are derived from old structures that go right back to the beginning of the vertebrate series.

Para. 62. The partitions between the clefts possess not only skeletal parts, they possess a definite musculature for the movements of the parts of the arches against one another and against the head, nerves which supply the muscles, skin and mucous membrane, and vessels which carry the blood to and from the gill apparatus.

In a fully functioning gill all these parts are used in the service of respiration. The muscles act as constrictors and dilators and as adductors of individual parts of each arch.

The vessels carry to them blood rich in carbonic acid and carry away blood rich in oxygen, the nerves bring about the movements of the muscle and provide sensibility for the outer skin and mucous membrane and regulate the calibre of the blood-vessels. However, the visceral arches persist as elements in the structure of the head, and though still respiration is no longer in being, the visceral muscles, nerves and blood-vessels still persist and form basic elements of the human head and neck. Without a knowledge of this transition these elements would form something very mystifying and difficult to understand. The demonstration of these homologies and relationships makes possible a clear insight into this organization.

The original form of the visceral musculature (fig. 24) is a sling muscle encirling the arch, which is divided in many ways into a dorsal and ventral portion.

The origin and insertion lie in the richly divided visceral skeleton (particularly as dorsal and ventral constrictors). Noteworthy are the elevators of the arch which arise from the second uppermost element of the arch. The whole muscle is distributed topographically along the arch to which it belongs, so that we distinguish muscles of the mandibular arch, of the hyoid arch and of the succeeding arches.

The allocation of a nerve to one of these arches, and, of course, to the musculature of the arch, fixes the grouping beyond doubt. It is not possible to follow in detail here the fate of this musculature which stands in such intimate relationship with the differentiation of the arch as has been described. The result as it happens in man can easily be surveyed (fig. 25). The constrictor group of the mandibular arch becomes the starting point of all the muscles of mastication, also for the mylohyoid and the anterior belly of the digastric, and further, for the tensor veli palatini and the tensor tympani. All these muscles are supplied through the mandibular branch of the trigeminal. Out of constrictors of the hyoid arch arises the skin musculature, which becomes widely distributed over the neck, face and head (platysma and masculature of the scalp). From the dorsal constrictors of the hyoid arch arise the stylohyoid and the posterior belly of the digastric as well as the stapedius, all these being supplied by the facial nerve. To the third arch the levator veli palatini belongs and represents the dorsal constrictor, as do also the styloglossus and the stylopharyngeus. These are supplied by the glossopharyngeal. From the last constrictors arise the musculature of the larynx, dilators such as cricothyroid and the cricoarytenoideus posticus, sphincters as cricoarytenoideus lateralis, thyreoarytenoideus, interarytenoideus transversus. These lie in the region of the vagus

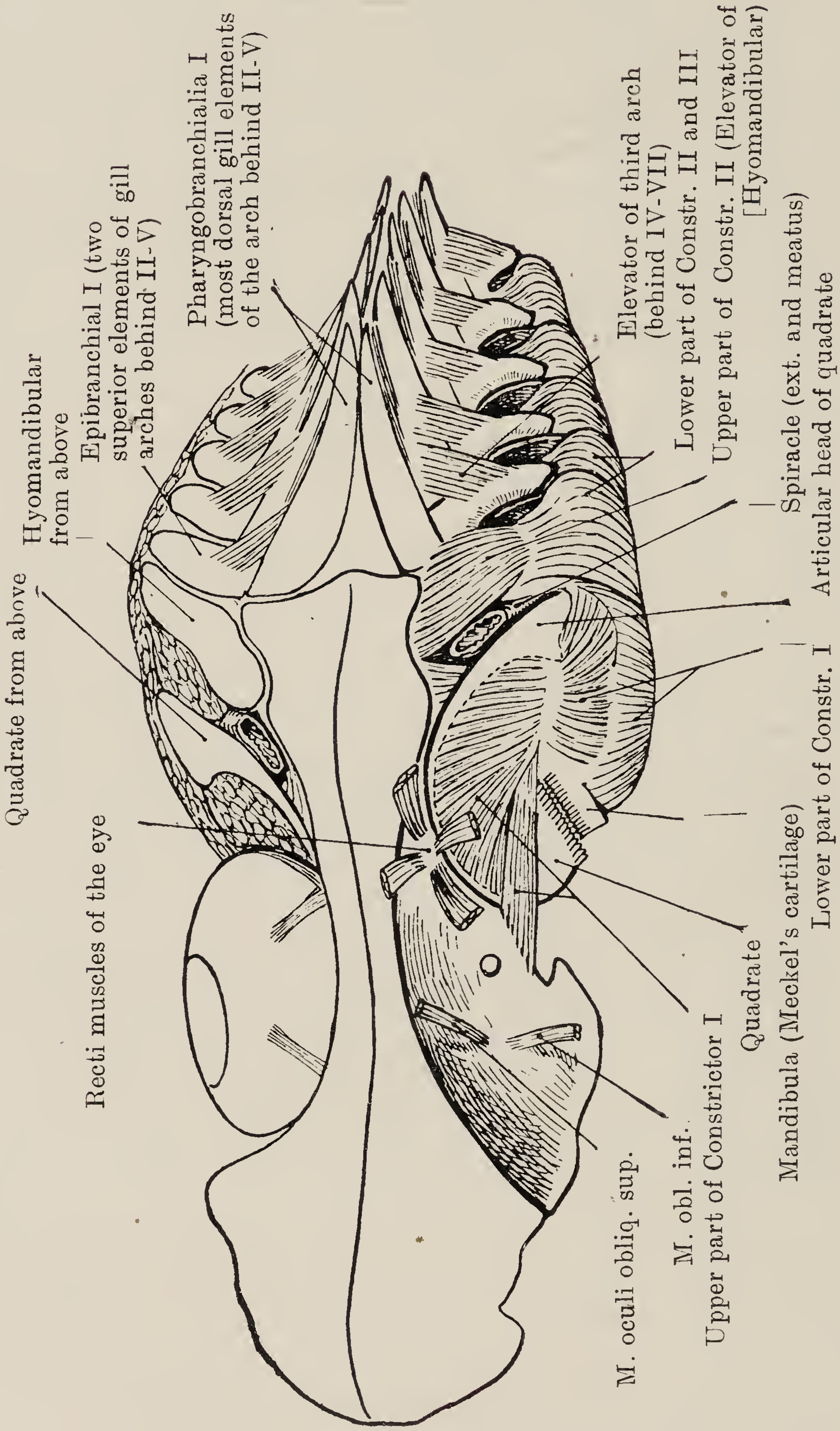
Quadrate from above
Hyomandibular from above
Epibranchial I (two superior elements of gill arches behind II-V)
Pharyngobranchialia I (most dorsal gill elements of the arch behind II-V)
Recti muscles of the eye
Elevator of third arch (behind IV-VII)
Lower part of Constr. II and III
Upper part of Constr. II (Elevator of [Hyomandibular)
Spiracle (ext. and meatus)
Articular head of quadrate
Lower part of Constr. I
Mandibula (Meckel's cartilage)
Quadrate
Upper part of Constrictor I
M. obl. inf.
M. oculi obliq. sup.

Fig. 24.—View of the head of a ray (Acanthias) with the visceral muscles represented. On the left the bulbus oculi is removed. The clear spaces between the upper and lower parts of Constrictor I is an intermediate tendon traversing the constrictor. The muscle parts joined throughout are presumably homologous with the internal pterygoid of mammals.

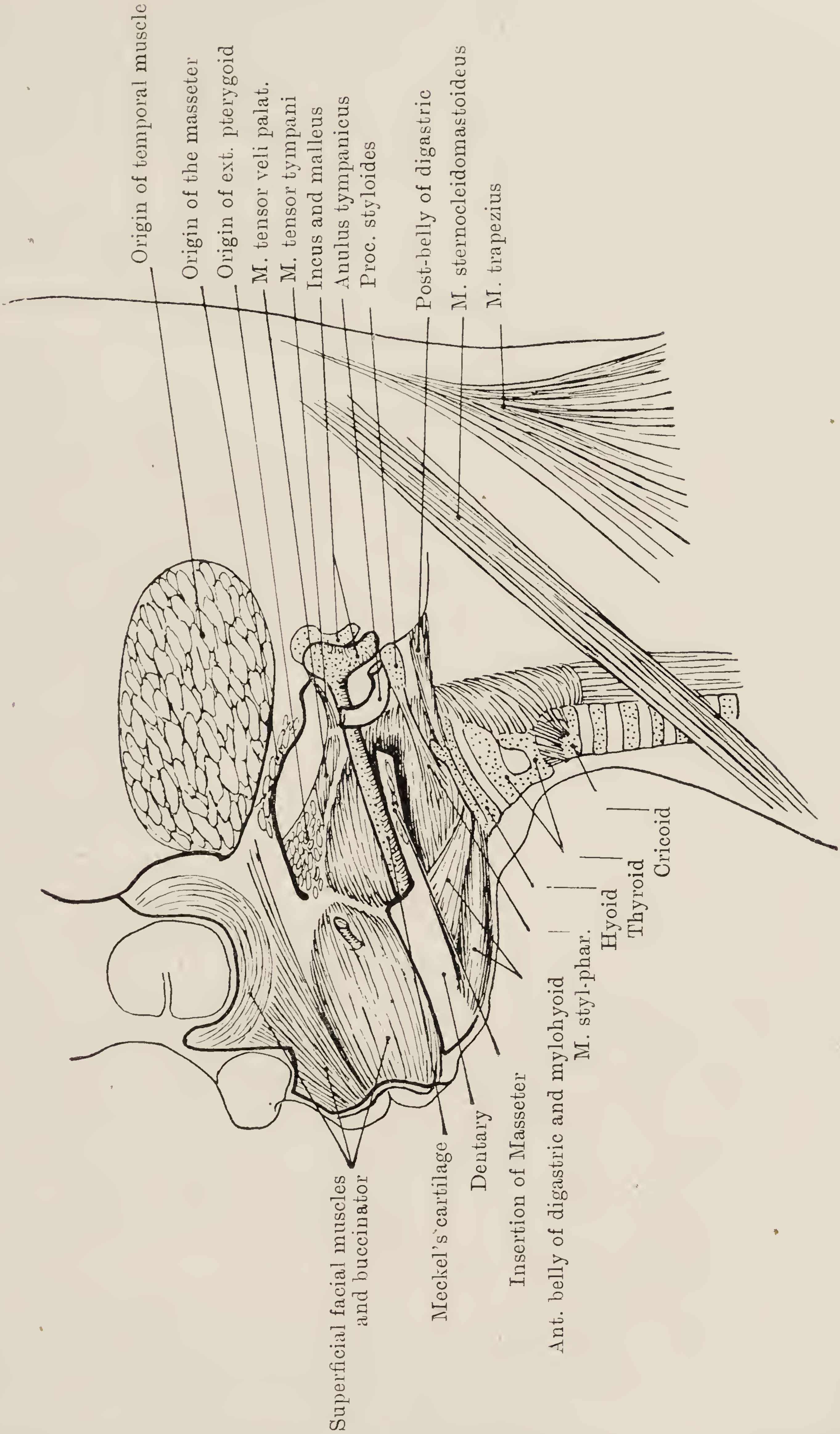

FIG. 25.—Gill arch musculature of man. The bony lower jaw is removed. Meckel's cartilage ends as the head of the malleus, the quadrate as the incus. The greater part of the tympanic ring has been removed.

(superior laryngeal) and accessory (ramus internus = n. recurrens). The whole of the constrictors of the pharynx belong to the third arch (nerves nine and ten) whilst the sterno-mastoid and the trapezius belong to the important levator group of the posterior gill arches (ramus externus of the accessory).

In order to understand the anatomy of the human head it is important to realize that the musculature of the second arch migrates superficially to that of the first, thus bringing also the facial nerve into a superficial position. The remainder present no special difficulty for their homologies are early recognized.

With the establishment of these visceral muscles it is not possible to find in the head muscles homologous with the trunk elements. On the contrary the question arises: what are the origins and homologies of these visceral muscles with the trunk musculature? The muscles of the trunk arise from myetomes. Is there muscle of similar origin in the head? The mesoderm extends from the trunk into the region of the head. We have seen that its differentiation from the myotomes does occur though only feebly. However, visceral musculature is not so derived. Also there occurs a division of the ventral-lying mesoderm into two layers with a space between them which stands in connection with the pericardial cavity and through this with the cœlom (fig. 17).

The presence of this head cavity suggests quite definitely that the head is a more differentiated trunk. If the head is an entirely new formation there is nothing that could explain the presence of these rudimentary spaces which never develop into any sort of individual space. The head cœlom is not a single space like the trunk cœlom. Since the gill slits occupy an intermediate position, there arises a series of slit-like sacs, each of which belongs to a visceral arch. Of much more significance as a criterion of the formation of the head is the fact that a true cœlomic sac arises below the optic vesicle in front of the mandibular cavity in the region of the maxilla. This, from its position, has been described as the pre-oral head cavity. This pre-oral cavity differs from the visceral arch (in regard to the pre-oral skeletal parts previously mentioned) in that, in consequence of the formation of the mouth cavity, it lies in front of the mandibular arch and the mandibular arch takes no part in its formation. [Balance paras. 29, 30.]

The walls of the cavity and not the visceral arch afford the material for the development of muscle, a development which is of the highest significance for the understanding of the formation of the head. In the trunk there is nothing resembling the visceral musculature; the material which gives rise to the cœlomic epithelium is the only material in the trunk which gives rise to the smooth muscle of the gut. One recalls that the gut is continued right into the pharyngeal region of the visceral arches, and so striking is this relationship that one might say that in the region of the closed gut unstriped muscle arises from the mesoderm of the splanchnopleure, whilst in the region of the arches the mesoderm gives rise to striped muscle. It is questionable, however, if we are correct in regarding one as the continuation of the other. It is possible to assume that the same mother substance in response to the movements of the gut gives rise to different structures. In man a transition between both types of muscle takes place in the œsophagus. Striped muscle is found mixed with smooth muscle as far as the stomach. These facts become of great significance for the understanding of cranial nerves.

Two groups of muscles have not yet been considered—the eye muscles and the tongue muscles. Both groups are sharply separated from visceral muscles, in that they are myotome muscles, comparable to those arising from myotomes in the trunk region. The eye muscles are developed from myotomes that lie in front of the otic vesicle. It is to be noticed, however, that unlike the trunk the head cavities are the primary structures and the myotomes grow out from the walls of the cœlemic sac (fig. 17). Until recently the presence of myotomes for the anterior head region has been denied and the eye muscles were thought to be formed from the wall of the cœlomic cavity. It is apparent from the innervation of the eye muscles that they differ from the visceral musculature. This innervation is not derived from visceral nerves but comes from nerves which are homologous with the nerves of the ventral spinal roots (p. 222). The nerve of the pre-oral head cavity is the oculomotor. From the dorsal evagination of this head cavity is developed the musculature supplied by this nerve. The superior oblique and the rectus lateralis are developed from the dorsal part of the mandibular cavity. Whilst the fourth nerve occupies a special position, the sixth nerve, like the third, is in every way comparable to a spinal ventral root.

The musculature of the tongue in fishes and amphibia is only a part of the ventral trunk musculature, and is innervated by the first spinal nerve arising behind the cranium. The genioglossus and the hyoglossus are derivatives of the trunk musculature which come to lie in the floor of the mouth. Only in the amniotes does the hypoglossal nerve reach the exterior through the skull, and though it has been elevated to the rank of a cranial nerve it retains its spinal characters. These can be easily recognized. It differs from a spinal nerve only in so far as its sensory part is markedly reduced. It is in the main a series of motor roots with a spinal ganglion related chiefly to its last root. Its intimate relation with the spinal nerves is also indicated by the ramus descendens, which is nothing else than a loop which takes part in the plexus formed by the first three cervical nerves and the hypoglossal. The hypoglossal nerve supplies only the true muscles of tongue (genio-stylo- hyo-glossus, longitudinal and transverse lingual muscles), that is, muscles which are already present in the amphibian tongue muscles. Through the ramus descendens, i.e., through the first three cervical nerves, the ventral rectus system in the neck is supplied (the infrahyoid and the geniohyoid).

Para. 63. We will now proceed to the question of the cranial nerves and their relationship to the trunk nerves. As is well known, each mixed spinal nerve consists of a ventral motor root and a dorsal sensory root. From the eighth cervical to the second lumbar a sympathetic part runs in the anterior root.

The beginner should remember (also in the study of the cranial nerves) that the sensory root has its origin in the spinal ganglion, from which it passes into the spinal cord. This is essential for the understanding of the cranial nerves.

The ten cranial nerves which remain after the subtraction of the olfactory and the optic show another relationship. A part of them, namely, the oculomotor, the trochlear, the abducens and the hypoglossal are purely motor. The six others show a greater complexity. They contain a sensory portion as well as motor which supplies the visceral muscle. A further sensory element goes to the sense organs. Finally, the cranial nerves possess parasympathetic fibres which run in the oculomotor, facial, glossopharyngeal and vagus. In the comparison of the sensory parts of the cranial and spinal nerves there is full agreement. Also the cranial nerves possess ganglia which are of the same value as the spinal ganglia, and, of course, the sensory part of the trigeminus springs from the Gasserian ganglion, that of the glossopharyngeal from the ganglion petrosus, that of the vagus from the ganglion jugulare and the ganglion nodosum, that is, from bipolar cells.

In general the destination of these fibres arising from these roots is the "general skin system." They transmit, as do the spinal nerves, sensory impulses of the skin, mucous membranes and serosa : temperature, pressure, taste. In addition they transmit the impressions from the muscles and joints. Their central paths are the same as in the spinal cord, whose ascending and descending paths transverse the posterior columns of the spinal cord. In the cranial nerves there are found ascending and descending trigeminal, glossopharyngeal and vagus paths (tractus solitarius) ; their secondary neurones attach themselves to the fillet.

Sensory elements are contained in the acoustic and glossopharyngeal nerves. The end-buds of the latter are limited in all vertebrates in their peripheral distribution to the cavity of the mouth, to the gums, tongue and beginning of the œsophagus. The former is widely distributed in marine animals as the nerve of the neuromast organs. The neuromast organs (the organ of the sixth sense) lie in the head and trunk, in the lateral line system. The sensory nerves of this system arise from the facial, which in a narrow sense is no facial nerve but is called so in the fishes owing to the transference of the term from human anatomy. They extend from the trunk of this nerve widely through anastomosis with the trigeminus and the vagus. The acoustic is the special portion of this sensory group that supplies the neuromast organ (the macula and crista acusticæ and the spiral organ of Corti). Since in terrestrial animals the lateral line system is no longer present, so the facial becomes only a vestige of its former size. The acoustic is retained and it always arises and runs in the most intimate relationship with the facial. In addition it is necessary to know in order to understand the human facial nerve that it had in the head not only motor and sensory functions but also cutaneous connections. Originally it contained extensive fibres which innervated the mucous membrane of the palate (ramus palatinus VII).

The motor parts differ from the corresponding anterior roots of the spinal cord.

In the transformation of the spinal cord into the medulla the motor column of the anterior horn passes into the motor root of the hypoglossal. Further forwards the motor nuclei of the abducens and the oculomotor are topographically in the same position.

The motor portion of the other nerves, on the contrary, spring from a nuclear column which begins in the nucleus ambiguus (IX and X), and is continued in the same column to the nucleus of the facial and the trigeminus. The fibres also take a different central course from those of the twelfth, sixth and third. Whilst these, exactly as do the ventral roots of the spinal cord, run straight ventrally and issue ventro-medially, these others first pass dorsally and come into apposition with the sensory roots. This typical course is particularly striking in the case of the facial, whose loop forms a visible elevation or knee in the floor of the fourth ventricle. Their exit does not lie ventro-medially but dorso-laterally, generally close to the exit of the sensory part of the nerve. This is most clearly seen in the exits of the nerves from the medulla. The accessory follows this rule. The so-called accessory is only a part of the vagus. The spinal accessory, the accessory strictly, arises from a nuclear column in the anterior horn, which is serially homologous with the lateral nucleus ambiguus. Its exit in reptilia, birds and many mammals is in series with the dorsal roots (Lubosch). In higher mammals and man it is pressed more ventrally by the dorsal roots, but shows in many features of its course its association with the dorsal roots.

The following list of characters is of service in understanding the relations between the spinal and cranial nerves. The cranial nerves are distinguished from the spinal nerves in that: (1) Their motor roots remain distinct (somatic motor nerves). (2) Their posterior roots are not pure sensory but are mixed and are composed of sensory and viscero-motor fibres. This last-mentioned distinction is thus explained. The viscero-motor elements of the dorsal roots have become just as foreign to the trunk as the musculature of the visceral arches themselves. In respect to the first distinction, the state of affairs differs for the eye muscle and tongue muscle nerves. The twelfth, as already mentioned, is really only a spinal nerve arising out of three roots whose dorsal roots have undergone marked atrophy. Where the dorsal roots of the ocular nerves are to be found is still unsolved.

When comparing the nerves of the brain and spinal cord we must not forget that agreement of position does not exist in one very important particular: The roots of the cranial nerves run above the head myotomes and separate, in the course of evolution, with their ganglia from the ectoderm, while the sensory roots of the trunk nerves run below the myotomes and their ganglia separate from the spinal cord. The embryonic primordia of the cranial ganglia and of the trunk ganglia do not fall together but run side by side in the hind cranial region (Froriep, 1901). There is thus no complete homodynamy of cranial nerves and trunk nerves. Nor do they arise successively from the union of trunk nerves, but, like the primitive cranium, they represent for existing vertebrates something given and perfected (Gegenbaur, 1887). It is only in the occipital section that we can recognize an actual change of trunk nerves into a cranial nerve (N. hypoglossus).

When we speak of cranial nerves we must remember (Gegenbauer) (leaving out the olfactory and the optic) that they arise from only a very limited part of the brain. In primitive forms like the cyclostomes they all arise from the hind-brain (medulla oblongata), but in the higher forms the ocular nerves as well as part of the trigeminus have an origin from the mid-brain. In general, one may say, however, that the cranial nerves belong to the medulla oblongata, having regard to their primitive position. This is also the part of the brain that shows in its development the clearest appearance of segments which, therefore, must be regarded as the part most closely approximating in form to the arrangements of the nervous system of the trunk. Herein it is only partly clear what neuromeres correspond to individual nerves, and if and how far these neuromeres correspond to the myotomic arrangement of the posterior part of the head.

Para. 64. When we survey the extent of the cranial nerves we see how their primitive arrangement helps to explain their distribution. In general we may say that each mixed cranial nerve possesses two branches which run in front and behind the gill opening, the ramus pre-trematicus and the ramus post-trematicus. The first is always purely sensory; the second, which supplies the musculature of the arch, is mixed (trema = lake) (fig. 22, *a*, *b*).

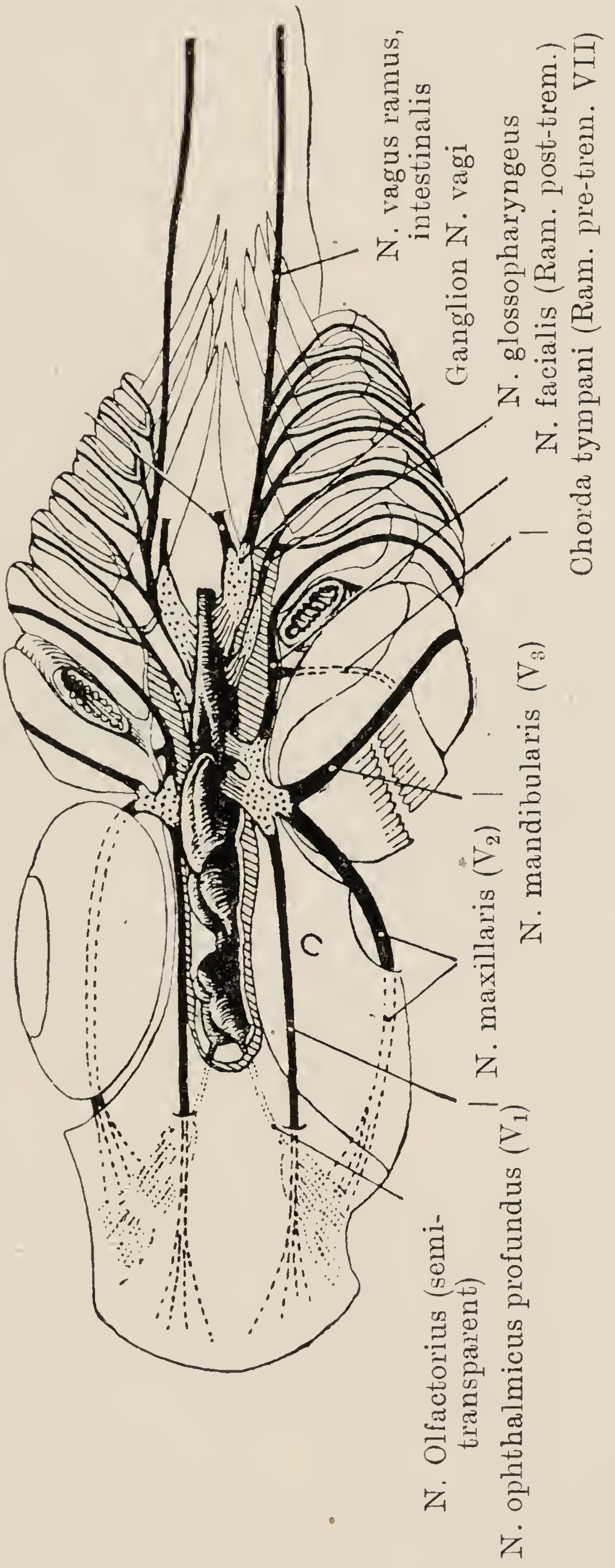
N. vagus ramus, intestinalis
Ganglion N. vagi
N. glossopharyngeus
N. facialis (Ram. post-trem.)
Chorda tympani (Ram. pre-trem. VII)
N. mandibularis (V_3)
N. maxillaris (V_2)
N. ophthalmicus profundus (V_1)
N. Olfactorius (semi-transparent)

Fig. 26.—The skull of a shark opened to show the brain. Nerves of the gill arches. The ganglion of the fifth and the seventh lie together. In the seventh, ninth and tenth cranial nerves a ramus pre-trematicus and post-trematicus. Ramus pre-trem. of the seventh nerve = chorda tympani. Ramus lateralis of the vagus removed.

The trigeminus only becomes in the higher animals a nerve of three portions. Originally in cyclostomes and fishes and even in amphibia it is a nerve of two parts only. The anterior part runs along the medial wall of the orbit as the nervus ophthalmicus profundus. It is the nerve of the ethmoidal region and in man is represented by the nasociliary. The caudal portion supplies the first visceral arch and its muscles (ramus post-trematicus = nervus mandibularis). The lingual and buccinator are branches from it to the mucous membrane. There is a superficial branch which runs above the eye and in human anatomy is known as the ramus ophthalmicus, and a pre-trematic branch to the skin and mucous membrane of the superior maxilla, the ramus maxillaris.

Since the oculomotor in many primitive and in some higher forms carries sensory fibres and bears the ciliary ganglion, which in man and in mammals contains predominantly cells of the sympathetic system, it has in more primitive forms probably the character of a spinal ganglion (bipolar ganglion cells). Since further the ocular muscle takes origin from the wall of the pre-oral head cavity the opinion has been expressed (Gegenbaur) that the ophthalmicus profundus (nasociliary) is the nerve of the pre-oral head segment, and the oculomotor corresponds to its ventral motor root. At any rate, this would explain the association of the nasociliary and oculomotor with the ciliary ganglion. In the same way from the relationship of the lateral rectus to the mandibular cavity (p. 218) the opinion has been formed that to the posterior trigeminal complex, that is the nerve of the mandibular arch, the abducens belongs as the somatic motor root. If we could be sure of these things then one could regard the trigeminus complex as the final result of a process of the subordination of the head cavities to the visceral arches. Its nerve and its musculature would fuse together into a unit with the more posterior nervous elements which we now describe as the "trigeminus."

The nervus facialis, if we ignore the sensory fibres which it possesses in water-living vertebrates, is like a mixed dorsal root. Its motor part has been described above; its sensory portion forms in part the separate nervus intermedius. Its spinal ganglion is the geniculate ganglion—whose peripheral fibres run in the second division of the trigeminal and through it to the sensory nerves of the mouth (sphenopalatine nerve). They correspond to the already mentioned ramus palatinus which the facial nerve, in its original form, possesses as an independent branch. Like each cranial nerve the facial nerve gives off a ramus pre-trematicus, which runs to the anterior boundary of the spiracle (ear cavity).

This branch lies medial to the mandibular joint (between Meckel's cartilage [articulare] and the quadrate as the nervus mandibularis in figs. 22 and 26). In the same position in man we find the chorda tympani (fig. 27) (from the posterior border of the middle ear to the anterior border between the malleus and the incus crossing the anterior process of the malleus [Meckel's cartilage] through the Glaserian fissure to the third division of the trigeminus).

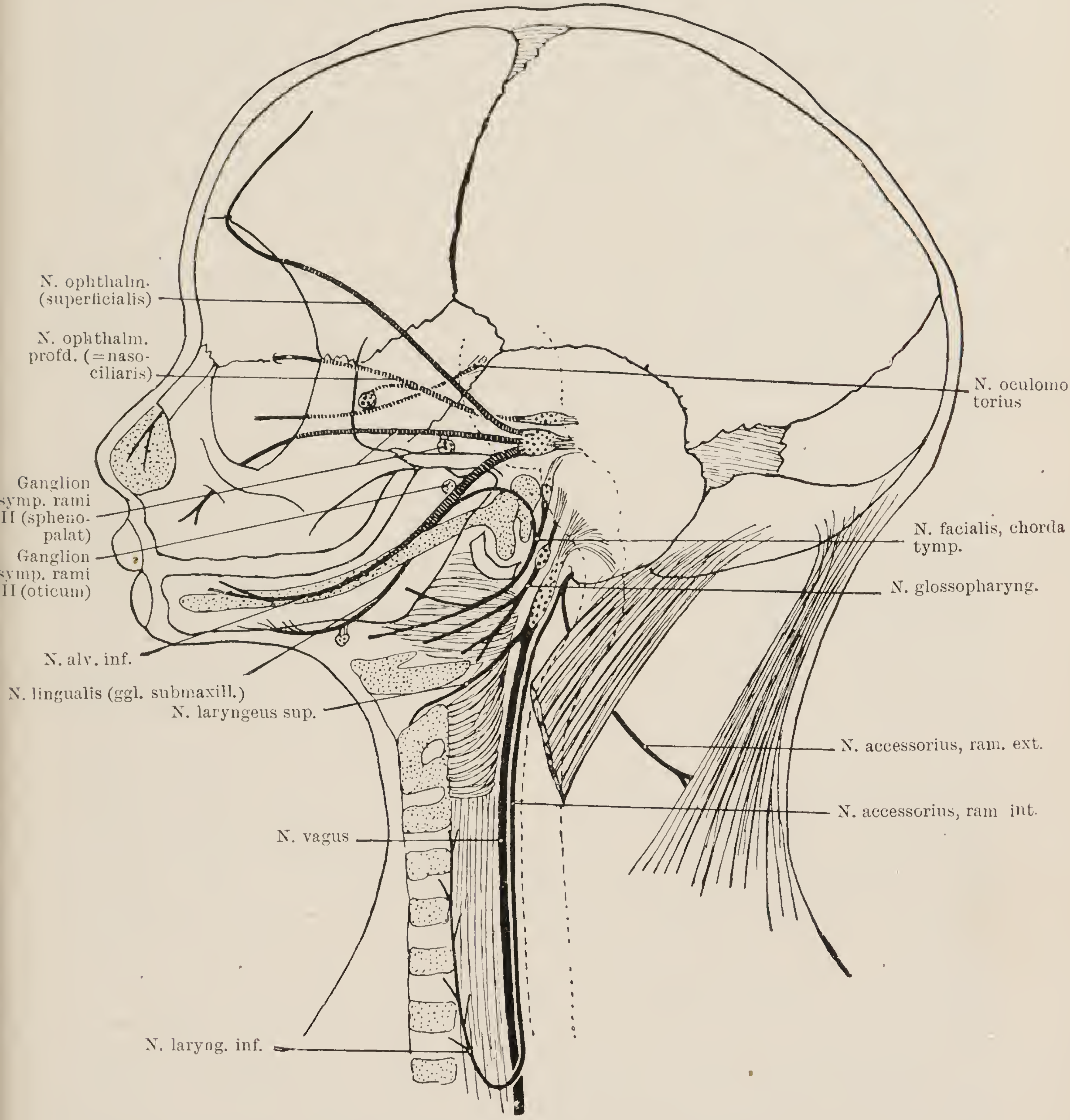
N. ophthalm. (superficialis)
N. ophthalm. profd. (=naso-ciliaris)
Ganglion symp. rami II (spheno-palat)
Ganglion symp. rami III (oticum)
N. alv. inf.
N. lingualis (ggl. submaxill.)
N. laryngeus sup.
N. vagus
N. laryng. inf.
N. oculomotorius
N. facialis, chorda tymp.
N. glossopharyng.
N. accessorius, ram. ext.
N. accessorius, ram int.

FIG. 27.—Nerves of the gill arches. Human. The nasociliary is shown as an independent nerve, the anterior trigeminal division (N. ophthalamicus profundus, see text); only the position of the oculomotor is indicated. The sympathetic ganglia of the head are schematically placed in the neighbourhood of the nerve trunks. Where the nerves are exposed they are black, where they are covered by bone they are stippled lightly.

Of the posterior cranial nerves only the vagus requires further mention. If one would understand its form and distribution one has to start from the fact that it is the equivalent cf a mass of visceral nerves, indeed as many as are comprised in the visceral arches that lie behind the third. To this is allocated the glossopharyngeal nerve, (the third visceral arch = the first gill arch) to the following arches the individual branches of the vagus in the fish. Of these the branch to the fourth arch of the fish corresponds to the superior laryngeal nerve of the amniotes. Also the nerves belonging to the fifth and sixth arches form, in the reptiles for example, laryngeal nerves. The nerve of the seventh arch corresponds to the inferior laryngeal in the amniotes (see below).

The spinal ganglia of the indivdual branchial nerves are fused to a single ganglion, the ganglion nodosum (and in part to the ganglion jugulare). Behind the last gill the ramus intestinalis of the vagus runs to the fore-gut. It is questionable if it is correct to call this continuation "vagus." Of the whole complex the vagus ought to be restricted to that part which derives its motor fibres from the nucleus ambiguus. This would include the area innervated by the spinal accessory which, besides the laryngeal muscles, supplies the upper part of the œsophagus, probably the striped muscle of this area which, regularly arranged in the upper third, reaches, though scattered, as far as the stomach.

The more caudal part of the vagus would be described differently (parasympathetic). The sensory portion of the glossopharyngeal and the vagus are distributed to the mucous membrane of the ear, tongue, larynx, pharynx and œsophagus. The sensory nerves of the mucous membrane of the gut run, as we know, not through the vagus but through the sympathetic. This would become understandable from the morphology of the vagus as has been described. Only a single cutaneous branch arises from the vagus, the auricular nerve of Arnold. This is the tiny remnant of the static vagus branches in the fishes which supply the skin of the trunk as the lateral line fibres. The ganglion of this nerve is the ganglion jugulare of the vagus.

We have dealt with the typical portions of the cranial nerves, the plan of their arrangement and the principles of their distribution, but we have yet failed to consider the parasympathetic portion, which, as above remarked, is peculiar to the cranial nerves. There does not, however, arise here any fundamental divergence. This is shown by the existence of the sacral parasympathetic. As the whole knowledge of the parasympathetic system is of recent date there is as yet nothing known of its arrangement in the primitive vertebrates.

From analogy of the relationship in man and the mammals we can only guess that special parts of the facial, glossopharyngeal and vagus described as sensory fibres are of a parasympathetic nature. Since each cranial nerve, leaving out the trigeminus and the hypoglossal (these as cranial spinal nerves cannot be considered), have parasympathetic portions, this peculiar distribution fortifies the opinion that the oculomotor belongs to the trigeminal group. The parasympathetic portion of the oculomotor running as in a ventromedial root occupies a special position which, formally considered, remains as yet unexplained. The final distribution is also quite unusual and without homology. (The smooth muscle of the sphincter pupillæ and the ciliary muscle.)

The relationship of the remaining cranial nerves is clear. Salivary glands and smooth muscle are the destination of the parasympathetic fibres. A nucleus salivatorius lying in the medulla is the origin of the nerves of the first group. These run in the centrifugal part of the nervus intermedius and the glossopharyngeal. They join with the ramus palatinus of the facial (the great superficial petrosal nerve) with the first and second divisions of the trigeminus; through the ramus pretrematicus of the facial, the chorda tympani, with the third division of the fifth; through the lesser superficial petrosal nerve with the otic ganglion (auriculo-temporal and buccinator nerves). Thus all the glands of the head acquire a special innervation and are mainly supplied by the facial (Nauck). A second parasympathetic nucleus is represented by the cardiac nucleus of the vagus (small-celled vagus nucleus) from which the cardiac branches of the vagus arise. One ought not to reckon these fibres as part of the vagus any more than one does those fibres which go to the smooth muscle of the trachea, bronchi, œsophagus, stomach, gut, etc. They are situated in the vagus without belonging to that conception which limits the vagus to the parts belonging to the visceral skeleton. The place of origin of these gut fibres is uncertain. It is also uncertain whether these parasympathetic fibres are interrupted in the ganglion nodosum and therefore are post-ganglionic fibres (R. R. Müller), or if they go straight through the ganglion as preganglionic fibres and are first interrupted in the cœliac ganglia (Elze).

Para. 65. The arrangement of the arterial vessels is closely bound up with the form and development of the visceral arches. They are distinguished from those head portions which we have already considered in this, that they topographically belong to the head only in a small degree. This distinction is founded on the fact that the central vascular organ, the heart, is situated in the trunk; therefore in a region caudal to the visceral arches, between the first development of the arteries of the head and neck in man and their position in the gill-breathing animal, there is so close an agreement that without any reflection we can assign to this the explanation of their relationship in man.

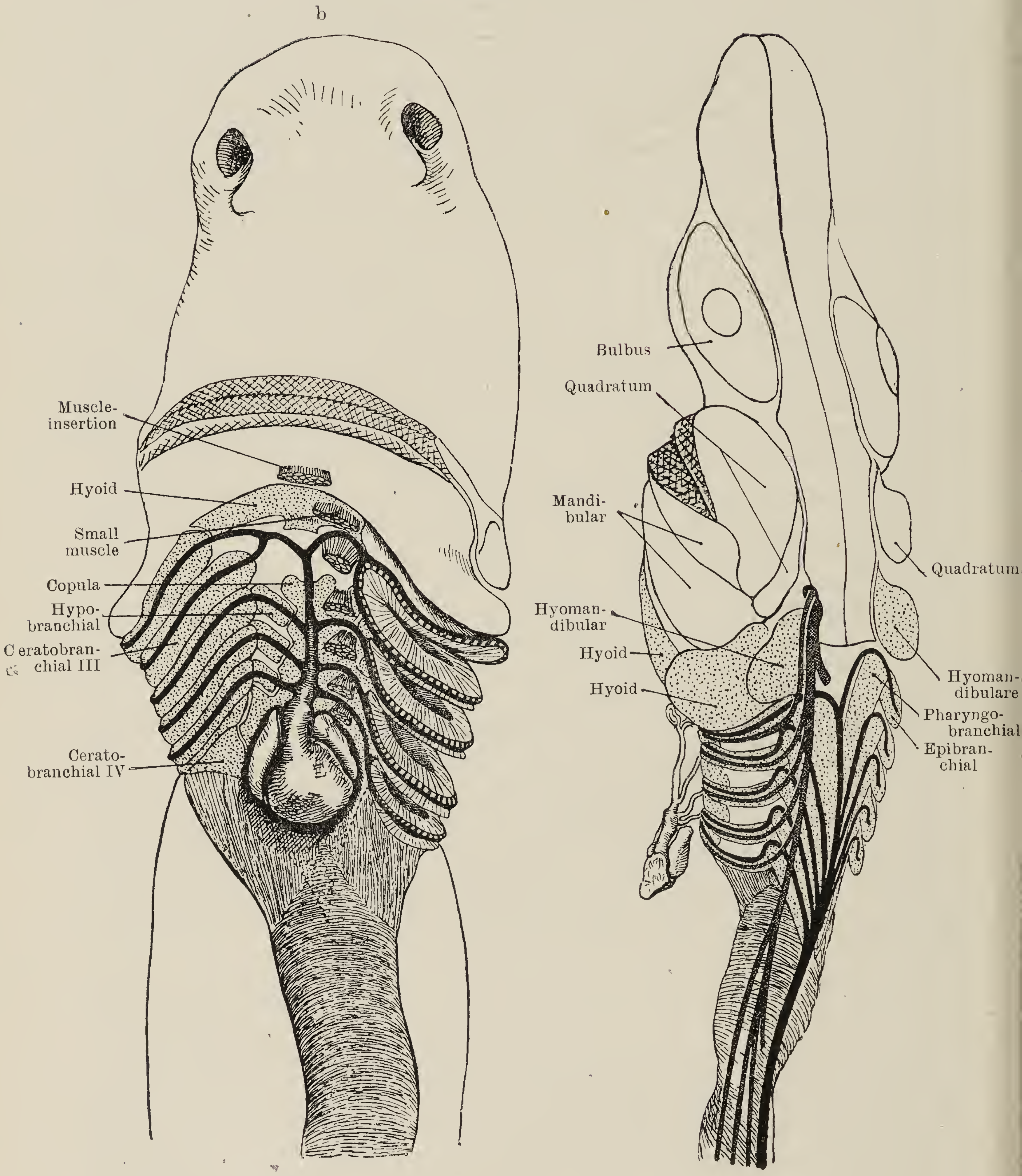

Fig. 28.—Head of a ray (Acanthias) with heart and the vessels of the gill arches (aortic arches). The vessels of the two first gill arches are not shown. (a) from the side with the glossopharyngeal and vagus nerves ; only their rami post-trematici shown ; these run in front of the corresponding arteries. Junction of the arteries to form the dorsal aorta ; (b) viewed from below.

The pharynx (figs. 28, a and b) which is continued into the œsophagus, is markedly increased in width and opens to the exterior through the gill slits. Ventrally in a deep fossa lie the pericardium and the heart. This gives off cranially the truncus arteriosus which carries venous blood to the gills. This shows through the gill arteries which, six in number, run to the hyoid and the five following arches. Here they end in respiratory capillaries (fig. 28, b) and from these on the dorsal side (fig. 28, a) arise vessels filled with arterial blood. Along the upper portion of the gill arches the vessels turn caudally and unite to form a longitudinal stem which runs caudally from the œsophagus as the dorsal aorta.

The unmistakable agreement with this plan is obvious in man (fig. 31, accessory fig.). The physiological distinction that arises in all lung-breathing vertebrates, that the whole system carries arterial blood, has no relation to the morphological aspects of the case..

In respect to the question of what is the relation of these arteries to the arteries of the trunk, we take up the same position which the considerations put forth above led us to, namely, that there are no homologues to them in the trunk. The arterial arches cannot, as has often been put forward (Corning), be the equivalent of the splanchnic arteries of the trunk. since these arteries arise from the aorta, which is situated dorsally, and run ventrally, whereas the aortic arches arise from the truncus arteriosus which occupies a ventral position and they first form the dorsal aorta (aortic arch = aortic root). They present, like the dorsal elements of the cranial nerves, an arrangement peculiar to the head.

The transformation of the aortic arches into the adult arrangement follows, in individual groups of vertebrates, differing paths. The schema (fig. 31) illustrates the process in man and the mammals. Generally applicable, and clearly in fishes, is the transformation of the two first aortic arches which are intimately related to each other, in that these arches do not give rise to gills, and further, that the vessels that belong to these are used for the nutrition of the eyes, the brain. and the tissues that envelop the brain. It would carry us too far to follow in detail the transformation of these arches. The third aortic arch on each side, the whole of the fourth left, the fourth right in part, and part of the sixth left persist. The fifth aortic arch early disappears. The ventral-paired longitudinal vessels (truncus arteriosus) persist throughout its whole extent. The dorsal between the third and fourth arches disappears; on the right side it disappears also on each side of the fourth. So arise the definitive vessels. The ascending aorta, the arch of the aorta, and the descending aorta (= common truncus arteriosus, fourth left aortic arch, dorsal aorta); the innominate artery (= fourth right aortic arch); the common carotid (= ventral anastomosis); the external carotid (= continuation of the ventral anastomosis) and the internal carotid (= third aortic arch + the remains of the dorsal anastomosis). The ductus Botalli is the sixth left aortic arch.

The growth of the neck and trunk drive the heart caudally. So the fourth aortic arch is displaced into the thorax whilst the third aortic arch (point of division of the common carotid) remains in the laryngeal region. A knowledge of these changes is essential for understanding the position of the nerves. The fourth post-trematic branches of the vagus (= laryngeal nerves, fig. 28, a) are so situated that they run in front of the corresponding vascular arches, that is, the superior laryngeal lies in front of the fourth arch, the two following in front of the fifth and sixth, the fourth branchial nerve (inferior laryngeal) belongs to the seventh visceral arch, and since this arch does not develop it lies behind the sixth. This is why the superior laryngeal reaches its destination from above and the inferior laryngeal from below. The differences between the recurrent laryngeals are also explained in this way, since the left must encircle the ductus Botalli (not the aortic arch, as is often erroneously stated), whilst on the right there is no ductus Botalli and the fourth aortic arch forms the innominate, which retains its position above the thorax in order to give rise to the formation of the subclavian. Of the two intermediate laryngeal nerves the third disappears without a trace whilst the second (nerve of the fourth entodermal cleft and fifth visceral arch) has been shown to exist at an embryonic stage in man (Dietrich).

(C) Morphology of the Neck.

Para. 66. The above has now brought us from the peculiar structure of the head to that of the neck. This raises the question what position this portion of the body occupies morphologically.

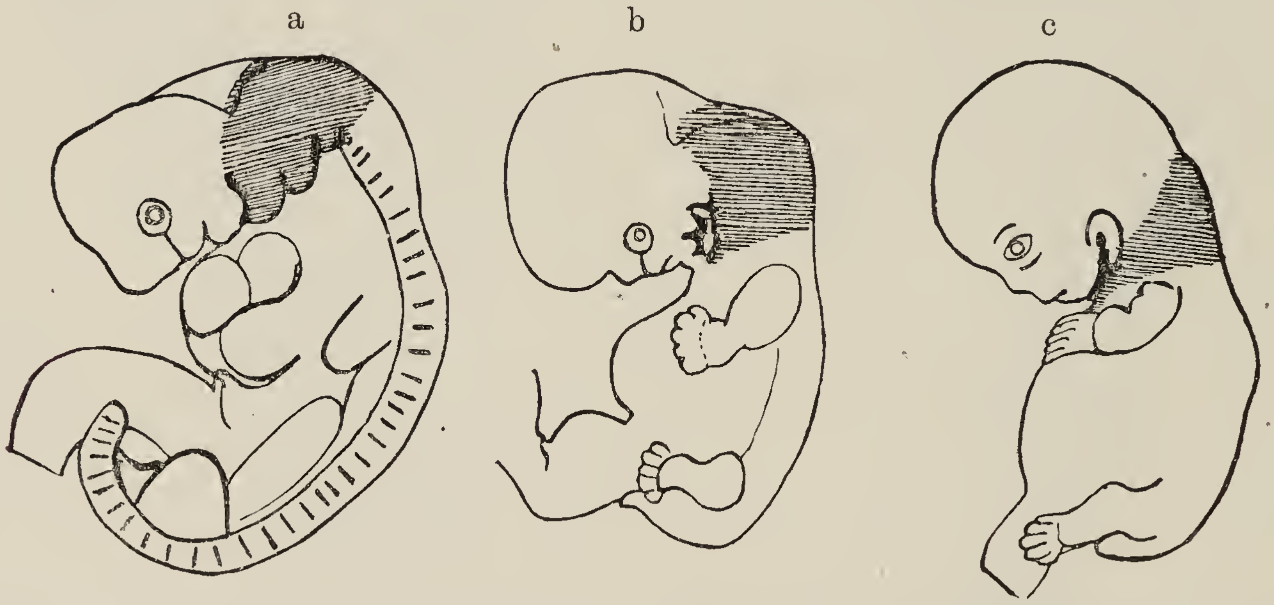

Fig. 29.—Three human embryos showing the development of the neck. (a) Embryo His K 10. Crown-rump length 10 mm. Age reckoned from 27-30 days. (b) His U 20, crown-rump length 14·5 mm. Age estimated at 37-38 days. (c) His W. 22, crown-rump length 16 mm. Age estimated at 42-45 days. All embryos and illustrations taken from Keibel (O. Hertwig's "Textbook," Vol. I).

We concern ourselves first with the fact that the neck as an outer limited portion of the body is present neither in the fishes nor in the amphibia, but is present in reptiles, birds and mammals. Internally the organization of a neck is already present in the amphibia since this has already acquired a free cervical vertebra, the atlas.

The function of a freely movable cervical vertebral column which allows the head to move would show how useful the neck is but

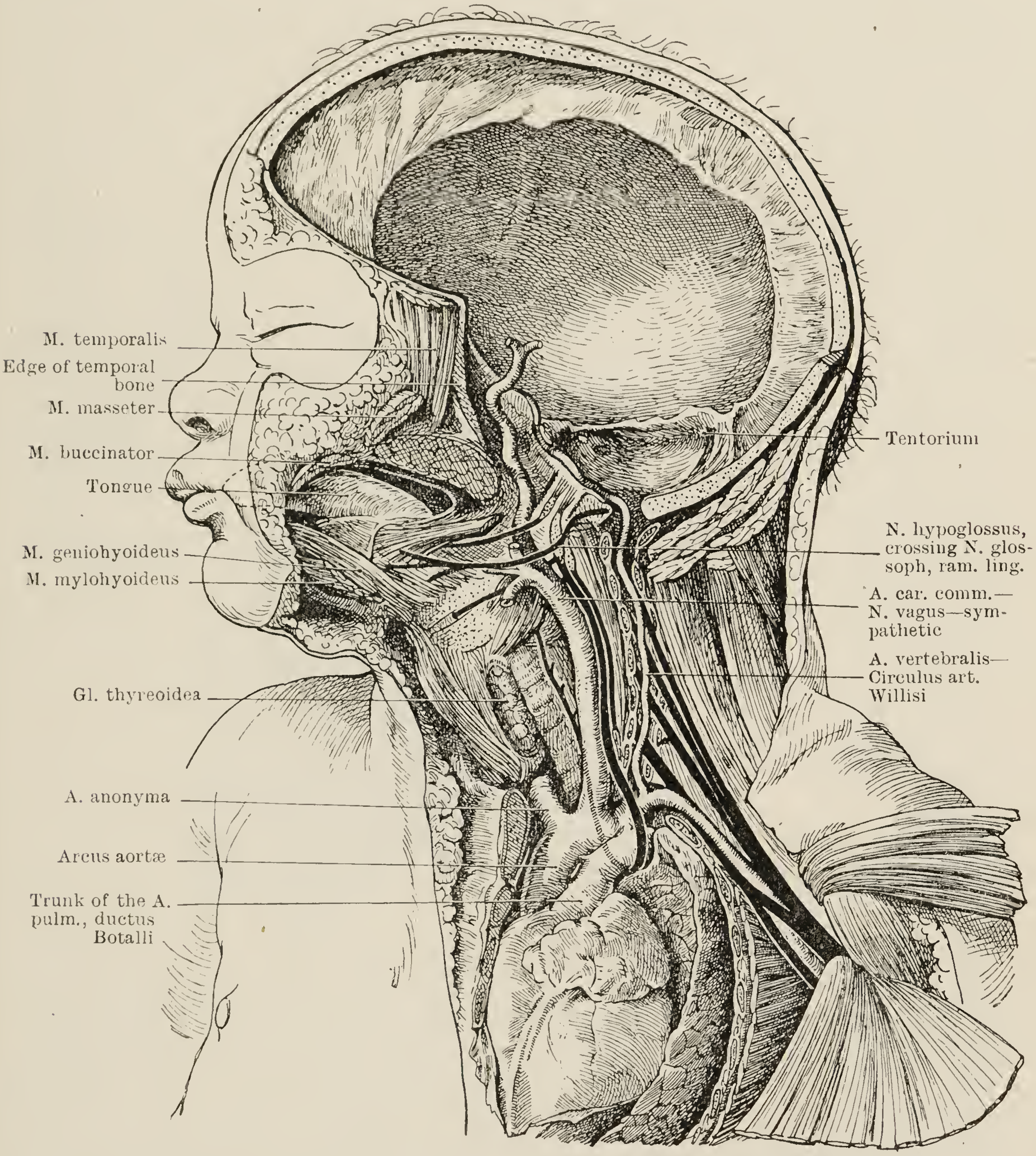
M. temporalis
Edge of temporal bone
M. masseter
M. buccinator
Tongue
M. geniohyoideus
M. mylohyoideus
Gl. thyreoidea
A. anonyma
Arcus aortæ
Trunk of the A. pulm., ductus Botalli
Tentorium
N. hypoglossus, crossing N. glossoph, ram. ling.
A. car. comm.—N. vagus—sympathetic
A. vertebralis—Circulus art. Willisi

FIG. 30.—New-born child drawn in proportion of 1 : 1·3. Reduced one-half in reproduction. Position of the transformed aortic arches.

would not explain why and how this portion of the body is formed. This explanation can be found only by considering the formation of the neck.

It is, in this regard, first of all proven that the neck only arises in those animals which possess an auximetameric skull. Here lies the key for the understanding of the neck. Through the approximation of material of the trunk to the head, the dorsal surface of the trunk is displaced towards the ventral region of the head in the position of the visceral arches, which in their turn are extended against the trunk (p. 214). The embryological expression of this displacement of the neck beyond the visceral arches is to be found in the cervical flexure of the neural tube (Rabl). Topographically, the cranial limit of the trunk area lies at the level of the hyoid bone over which lies the

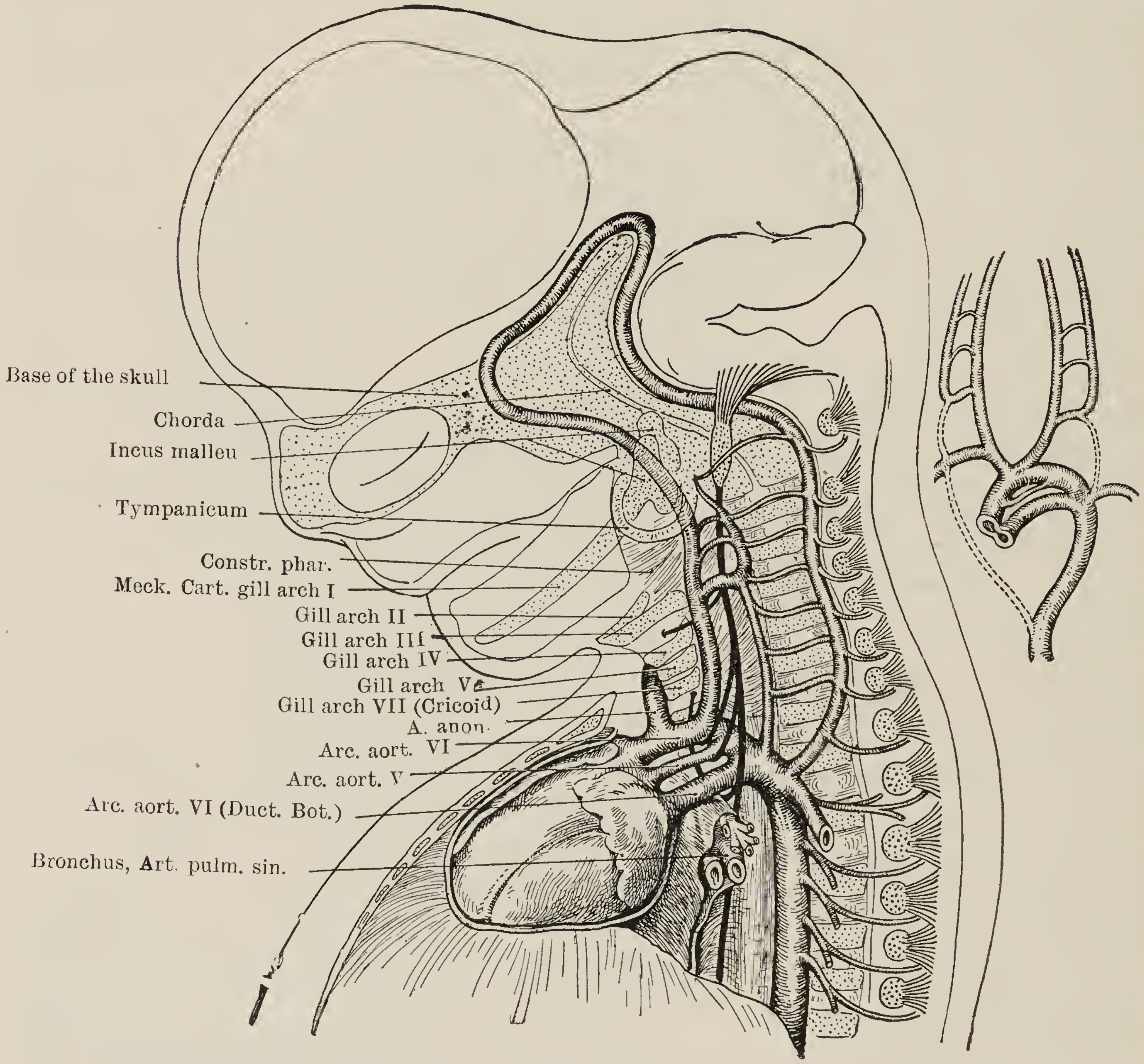

Fig. 31.—Human embryo of 3 mm., crown-rump length. Drawn in the proportion of 1 : 16. Reduced somewhat more than half in reproduction. The outline of the embryo, its thoracic viscera and nervous system, were drawn with a camera lucida. The vessels, nerves and vertebral column have been inserted schematically in order to bring the scheme into relation with the body (accessory drawing on the right). Four laryngeal nerves are shown ; the ending of the two middle ones, in order not to confuse the picture, are imagined to lie behind the common carotid. The trunk of the vagus, which is covered by the common carotid, is displaced laterally. The five aortic arches at this stage have long disappeared. They are here schematically retained. More detailed description of the figure in the text.

external ear. The further development carries the hyoid bone, owing to its great growth backwards, over the succeeding gill arches ("like the sections of a closed telescope"). The lower limit of this overlapping forms the cervical sinus. Still the ventral area is always shorter than the dorsal area. An external effect of this is that the chin always rests on the thorax. The heart is also carried further from the head. There is found therefore not a caudal movement of the heart, but instead an upward growth of the visceral region extended to about 90 degrees from the heart. So the neck is to be regarded as a result of a formative process by which the dorsal displacement of the trunk towards the head finds its expression on the ventral side. (So at least it appears ontogenetically) (fig. 29, a, b, c).

In the organogeny of the neck this process is clearly shown. The dorsal part belongs to the trunk and bears the features of the trunk. The ventral area is the visceral region and bears the characters of these structures. Here we find the visceral skeleton, the visceral musculature, the nerves (cranial nerves) and vessels developing from the aortic arches. The upper limit of the neck, if one can speak of such, lies between the mandible and the hyoid bone. In this the rectus system of the ventral trunk musculature reaches the lower jaw (musculature of the hyoid bone) and final consummation of the elements of the neck is brought about. In the typical unfolding of these parts it is well to recall firstly the retrogression of the cervical ribs, the retrogression of the entodermal grooves, and the formation of organs from the entodermal grooves and the ventral wall of the pharynx (tonsil, thymus, parathyroids, and thyroids), as well as the developmental history of the vertebral artery, which latter has still to be illustrated in outline (figs. 23, 26).

Also in the cervical region the aorta gives off arteries, the segmental arteries, which run to the occipital region (hypoglossal area) and to the cervical segments. With the former of these segmental arteries (the hypoglossal arteries), the internal carotid comes into connection along the base of the brain. Further, this junction starts a series passing backwards over the succeeding segmental arteries whereby the longitudinal stem is increased in length. The transverse portions of the segmental arteries disappear (the whole is shown in fig. 31) until the longitudinal stem (the vertebral artery) arises exclusively from the seventh segmental artery, that is the subclavian artery. In this elongation is expressed the backward displacement of the trunk material from the head. The displacement continues so long as new arteries are added to the vertebral until the proportions become stable. This gives the impression that the vessels are displaced caudally, but really it is the cranial portion which is elongated.

The original communication between the internal carotid and the vertebral is the posterior communicating artery and the basilar.

The anterior, the middle and posterior cerebral arteries are at first tiny side branches. So soon as these become large the original principal path becomes the posterior communicating. The anterior communicating arises later as an anastomosis between the two anterior cerebrals.

The narrowing of the ventral section of the cervical region and its form, as already described, are briefly influenced also by the fact that the whole myotome material of the fifth to ninth segment is situated caudally in order to take part in the formation of the musculature of the upper extremity. Only the small portion which is used in the formation of Mm. scaleni remains in the neck (Bolk, 1899).

(D) The Morphology of the Extremities.

Para. 67. Like the last portion of the body, the extremities afford examples of the principles in the construction of the body. Things quite unlike, and more difficult than in the head, meet us in the extremities. The extremities arise in two forms, the fins of fishes, the body appendages in land-living animals. The extremities are always present in two pairs, the anterior and the posterior (pectoral and abdominal fins, arms and legs). Though in marked contrast, yet the ground plan is easily recognized. There are three questions to be answered. Are the extremities derived from elements which arise in the body itself? Are fins and terrestrial limbs derived from the same elements? Finally, are the anterior and posterior limbs derived from the same elements?

The principal question is the first: It has been denied by many investigators. The conception has been advanced that Nature has brought forth from the lateral body wall this organ-complex for the purpose of locomotion. They begin as two lateral ridges or parachutes in which arise skeletal parts, muscle elements, and later blood-vessels and nerves grow into them from the body. The middle portion of this ridge undergoes retrogression, the beginning and the end persist. These ridges had served the fishes as balancing organs. In the land forms they became arms and legs (Rabl). Since these things have never been observed such a hypothesis can only be judged by what it explains and leaves unexplained. It does not explain chiefly the wonderful agreement in form between the arm and the leg, nor the separation into girdle and free extremity, nor the striking phenomena that the number of skeletal elements increases from the proximal to the distal segments, and the presence of the numerous (always ten in number in the beginning) supporting bones of the hand and foot.

It leaves unexplained the form of the shoulder-girdle as an arch surrounding the wall of the trunk and its division into dorsal and ventral parts (scapula dorsal, coracoid ventral — ileum dorsal, and ischium and pubis ventral). Finally, it leaves unexplained the fact which embryology shows at an early stage that the limbs are a unit, and that they begin with the differentiation of the shoulder-girdle. The older ideas of Oken, K. E. von Baer and Owen (Lubosch) had included the extremities in the unity of organisation, and doubtless recognized correctly that the general principle applied that true new formation is not found in animals, but only the unfolding of what is already present. Each investigator sees this presence in the ribs the starting point of the extremities. The ribs had, so one believes, become separate, and out of them has been derived the girdles of the limbs. Though much is thus explained, yet many things remain obscure. Before all, a free outgrowth of the extremities must arise with all their bones and muscles, blood-vessels and nerves, and the fundamental similarity of all these elements of both fore- and hind-limb must be the result of these events. K. E. von Baer saw another way open, for he perceived the similarity of the limb-girdles with the mandibular arch. On this process Gegenbaur later based his ancestral fin (archipterygium) theory, which is based not on the external similarity, but draws its support from important features of organization.

The ancestral form of the extremity is, according to this, the visceral arch. The extremities are modified visceral arches with differentiated appendages. The arch might be the ancestral form of the limb-girdle, its appendage, the gill rays, the ancestral form of the skeletal elements of the free extremity. The vessels and nerves are derived from that part of the ventral body wall in which the position of this arch is supposed to be. Indeed, parts of the true visceral arches as well as nerves are found in the region of the anterior extremity.

In fact, from a schematic representation, which may serve instead of long discussion, it may be well seen that, architecturally at least, fins as terrestrial extremities may be referred to an ancestral radial form as soon as one admits that one principal ray grows very much larger and the other rays are reduced to lateral derivatives from it (figs. 32, *b*, *d*, accessory figure)—ideas which are not beyond the realm of scientific postulates. Hereafter there can be distinguished a stem ray with double-sided (fig. 32, *d*) and one-sided (figs. 32, *b*, *c*, *f*) lateral rays (biserial and uniserial archipterygium). Both fundamental forms are developed in the vertebrates (figs. 32, *c*, *d*, *f*).

With the radial division there is joined in many ways a transverse division, most perfectly expressed in the terrestrial extremity, in which arises a division into stelopodium (humerus and femur), zeugopodium (radius and ulna, tibia and fibula) and basipodium (hand, foot skeleton) (figs. 32, *e*, *f*).

The derivation of the fins and extremities from an ancestral fin-like gill arch is founded on something deeper than mere external resemblance of form. It shows first of all in the position of the anterior extremity, which in fishes is always immediately behind the

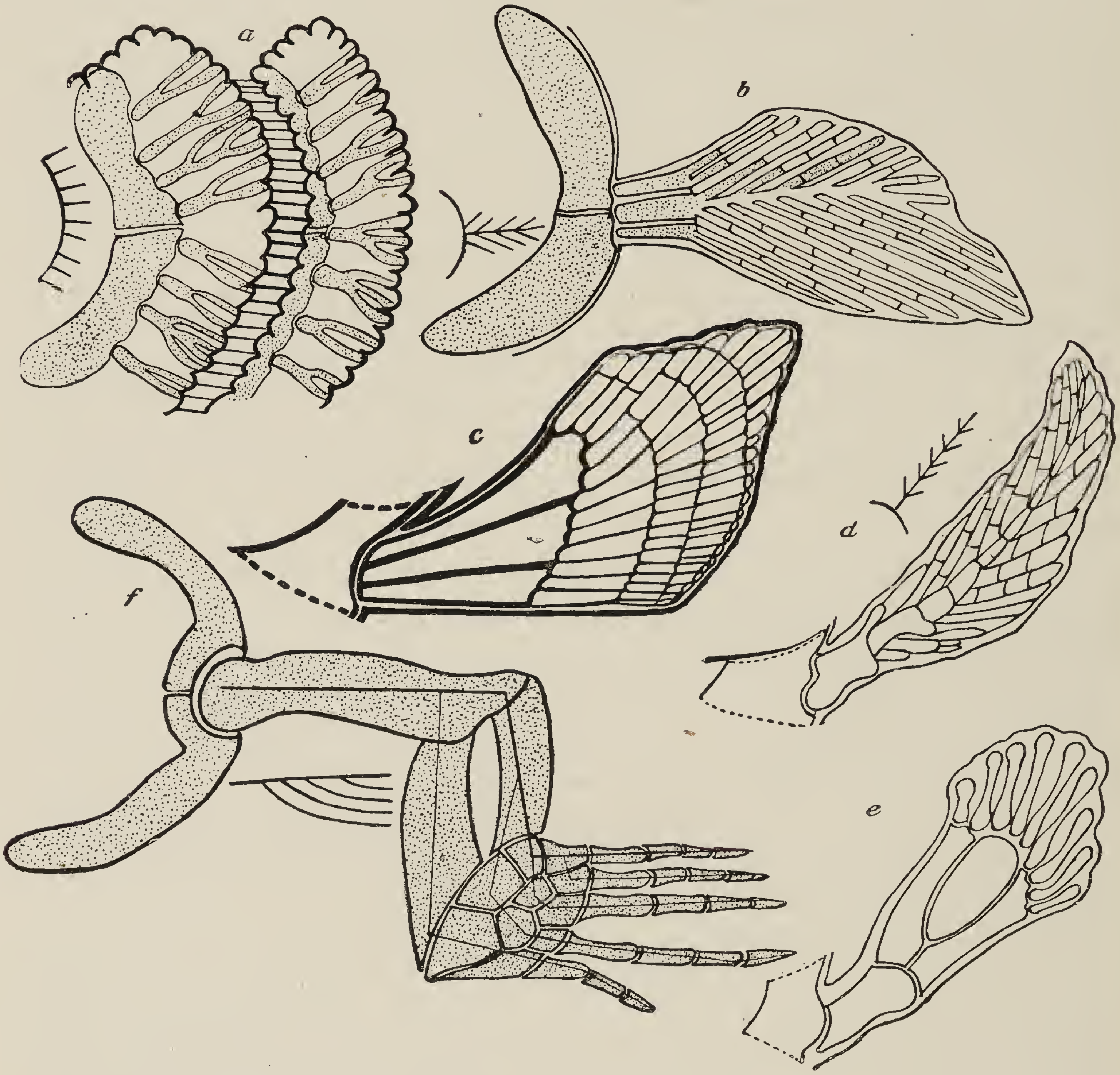

Fig. 32.—Schemes and sketches of the archipterygium theory. (*a*) On the left, scheme of a gill arch with radii; on the right, the radial skeleton of two gill arches. (*b*) On the left, a scheme, predominance of the middle rays; on the right, three rays which are inserted into the shoulder-girdle. (*c*) Conversion of Scheme 2 into the selachian fin. The three rays from below (in front) backwards (above) are the propterygium, mesopterygium, metapterygium. (*d*) Scheme of a biserial archipterygium. Only a principal ray with radii on each side. Example by the side sketched from the fin of Ceratodus. (*e*) The crossopterygian fin according to Klaatsch. A humerus with articular fossa, three distal elements of which two articulate with the humerus while all three articulate with terminal rays. (*f*) The extremity of a terrestrial animal referred to a uniserial archipterygium (one side possessing radii). The principal ray goes through the humerus, ulna and little finger.

gill arches, whose skeleton possesses intimate relations with the head skeleton. One observes that the limb-girdle exhibits a similar transverse division to that of the gill arches (p. 212), as also the fact above mentioned that actually vessels and nerves belonging to the visceral arches enter the girdle of the upper extremity (trapezius and sterno-mastoid, accessory nerve).

Admittedly, there are many more things in the extremities that cannot be demonstrated with certainty. Above all, the paths which the unfolding of the extremities have followed from the ancestral form. What we can interpret in the head with a fair degree of certainty is obscure in the case of the limbs. Probably the things lie so that each arch involved in the extremities was transformed and unfolded differently in different animal series, and so we can no longer make any statement as to how the extremities of the terrestrial animals were derived from the earlier developed fins.

Even so, it is necessary to believe that the arches of the anterior and posterior extremities lay close beside one another, and that the posterior had migrated from the anterior until it reached its final position. Though many facts in the anatomy of fins and extremities can be regarded in this light, it would suffice for our theory to accept that the formation of extremities had begun at that stage in animal organization when the visceral arches extended widely over the trunk. These in typical forms could have been various segments, so that in the comparison of the final state the appearance of having wandered might be suggested (p. 96). At the present stage of our knowledge it is not likely that we can solve this question on genetic grounds. The architectonic formal presentation of the homologies of the extremities is all that is possible at the moment and fruitful of any result.

As we must leave the question of origin unsettled, we will take up the analysis of the organization and test the archipterygium theory purely from a morphological point of view. If the skeletal rudiments as visceral arches are foreign to the trunk, then it must be allowed that they arise ventral to the ribs and must surround these laterally. This leads consequently to how the shoulder and pelvis girdles were formed anatomically. In the shoulder-girdle we have a ventral coracoid portion separated from a dorsal scapular portion. The scapula ends freely; the coracoid is united to the sternum. (Schema, figs. 34, 35.)

It is only in the higher mammals and in man that the coracoids have not these connections; it ends in these in the form of the coracoid process, and a dermal bone, the clavicle, places the scapula in relation with the sternum.

In the pelvic-girdle the ribs fail. The girdle attaches itself by its dorsal portion to the rib rudiments of the distal lumbar vertebræ which become the sacral vertebræ. The ventral portion joins with the opposite side and so completes the girdle. The ventral portion is divided into two parts by the obturator foramen, the cranial portion forming the pubis, the caudal portion the ischium. This arrangement is present in all the tetrapods.

In the amphibia and the reptiles a similar foramen is present in the shoulder-girdle as the coracoid foramen. The anterior bar of this is the equivalent of the pubis. The dorsal and ventral elements of the girdles have a special relationship to the articulation of the extremities. The joint surface is always situated at the junction of the dorsal and ventral elements.

The soft parts of the extremities must be derived from the trunk. This applies to the integument, muscles, nerves and blood-vessels. These all arise from the ventral part of the trunk and thus correspond to the ventral parts of a definite number of trunk segments. In the fins a whole series of myotome processes are demonstrable (Braus); likewise a definite series of ventral trunk nerves belonging to these myotomes and a definite series of segmental arteries. These fin myotomes do not retain their original independence, but give rise to new formations so that the corresponding nerves supply many of these radial fin muscles. This fusion of the myotomes in the formation of muscles leads to the production of the nerve plexuses (Eisler).

The extremities of terrestrial animals are somewhat similar, but many of their features are of a simpler kind. The extremities in these arise from the special development of a number of myotomes in their ventral portions. This applies to myotomes, vessels and nerves. The myotomes give rise to new entities in the musculature of the extremities. The segmental nerves by their fusion form new distributions through the plexuses. The plexus of the anterior limb is the brachial plexus and that of the posterior limb is the lumbo-sacral plexus. From the same segmental area arises the skin of the extremities, and their sensory and sympathetic nerves course in the same plexus, while the several segmental arteries are fused together to form a single main axial trunk for the anterior and posterior extremities.

Para. 68. From these illustrations there follows the possibility of demonstrating in a general manner the anatomy of the extremities. Polarity, symmetry, and metameric structure must be recognized as fundamental principles in the structure of the limbs as in the rest of the body, yet with special peculiarities inherent in them. The polar differentiation is very clearly shown in the skeletal parts of the limbs and is rendered very obvious through the functional subdivisions of these extremities. That the number of elements must increase as one passes distally in the limb is obviously implied in the ancestral radial form. The two skeletal parts, through one of which the axis of the limb runs, are the radius and ulna, the tibia and fibula. The small bones of the hand and foot, the carpus and the tarsus, are included herein. These in all terrestrial animals have originally numbered ten.

They are arranged in two rows (fig. 32, *f*) of which the proximal articulates with the zeugopodium whilst the distal bears the radial bones of the hand and foot. The proximal row comprises three bones, the radial, intermedium and ulnare, the tibiale, the intermedium and the fibulare. The five distal bones are the carpal or the tarsal I, II, III, IV, V. Between the two rows lie the two centralia, which make their number up to ten. These are arranged on the radial plan. This original form of the carpus and tarsus is schematically presented in the primitive amphibia. Numerous individual examples arise in which the individual bones fuse into larger complexes and thus afford greater variety in the range of movement by the alteration in the joint surfaces. The two centralia fuse into a single os centrale. In man where these bones have been described according to their resemblances, the os naviculare (scaphoid) corresponds to the radiale, the lunate bone is the intermedium, the triquetrum (cuneiform) is the ulnare. The os centrale does not normally persist but becomes fused to the ulnar side of the scaphoid or os naviculare. The carpalia I, II, III, are retained as the os multangulum majus (the trapezoid) and the os multangulum minor (the trapezoid) and the os capitatum (os magnum).

The carpalia, IV and V, fuse to form the os hamatum (unciform). These bear two metacarpals. In the foot the tibiale and the intermedium fuse to form the talus, whilst the fibulare forms the os calcis. The os centrale remains independent as the scaphoid. The I, II, III, of the distal row form the three cuneiforms, and the IV and V form the cuboid.

The metacarpals and the metatarsals form a further radial series, to which are attached the phalanges again arranged in radial fashion. The axial line is illustrated in the most movable lateral radius by the defect of the last phalanx (pollex and hallux) (fig. 32, *f*).

In respect to the symmetry [cf. also para. 48] each limb is the mirror image of the other. One may well ask why the number five governs the subdivision of each limb ? Purely mechanical considerations lead here to no real results, since only this number five is known to us, and suppositions based on the greater or less capacity of a three or seven-fingered extremity are valueless. Consequently we see in all terrestrial animals very wide reductions in the fingers, carpals and tarsals [mutation losses, para. 32], whereby even (deer, swine, hippopotami) and uneven (tapir, horse) numbers are produced. The supposition that unpaired axial digits are of particular value is worthless, since it does not hold in the case of the cleft-hoofed animals. It appears to be due to the extraordinary plasticity of the organism that the original pentadactyl form undergoes transformation due to function. Indeed the idea has become emphasized that the original form was a two-digit extremity (Rabl). We hold this opinion to be improbable, since we believe that the loss of structures once present may occur, but that there can be no new formation of a structure which was never present. One must recall that the "new formation" of a digit as an ancestral feature represents not only the outgrowth of a stump or the division of a rudiment, but the production of whole muscle-tendon nerve complex and affects the nuclear groups of the spinal cord and the brain and their central paths.

On these grounds we regard the pentadactyl extremity as an ancestral quality without cause, an archtectonic (promorphological) formative principle of terrestrial organisms. Surveying the facts that the hand and the foot which support the extremities and elevate the body from the ground become hypertrophied, and considering the double nature of the bones of the forearm, the triple arrangement of the elements of the distal part, the five-membered series of the hand and foot, and therewith the five digits, one could very well arrive at the impression of the need for the subdivision. These speculations, however, carry us beyond the limits of justifiable scientific speculation. There is no certain proof that the number of digits was once greater and has been reduced (prepollex and prehallux, post-minimus). The increase in the number of digits is always a malformation (usually an hereditary division of the primordium of a finger).

Another spatial relationship plays a great rôle in the extremity, namely, the dorso-volar arrangement. This is more important than the order of right and left.

Since the whole extremity lies within the ventral area of the trunk the terms dorsal and ventral ought not to be used in their usual significance. They would be better replaced by flexor and extensor surfaces (not to be confused with extensors and flexors, since there lie on the extensor side not only extensors but also supinator and peroneal muscles, and on the flexor side not only flexors but also pronator, tibialis posterior and others.) Both sides have become functionally different; the musculature of the extensor side strives to increase the angle of the elbow and the knee-joint (in man to abolish it altogether); hand and foot are held by them at an angle against the forearm and leg. The flexor muscles behave as antagonists so that both groups of muscles are concerned in each movement. In the limb-girdle where free movements prevail owing to the spherical shape of the joint surface, the muscle groups are so arranged that the arm and the thigh possess three principal movements about an axis, making with the principal axis of the body three planes perpendicular to one another. Owing to the combination of the action of individual muscles these movements can take place in any plane, arm and thigh being carried around on the conical surface. If this functional division of muscles on the flexor and extensor side is applicable to the whole of the free extremity, then it may be applied to the musculature of the girdles. A subordinate principle of classification is given clearly by the innervation. This method coincides with the division into flexors and extensors. This grouping is not functional but purely topographical.

In the plexus we can distinguish a division into dorsal and ventral portions. In the upper extremity the musculature innervated by the ventral divisions includes the subclavius, the pectorals and also the muscles supplied by the musculo-cutaneous, median and ulnar nerves. All the remaining muscles of the shoulder-girdle, except the tapezius and the sterno-mastoid (spinal accessory), as well as all the muscles (extensors) supplied by the musculo-spiral, are innervated by the dorsal divisions of the plexus. In the lower extremity only the psoas and all the tibial musculature are supplied by ventral divisions, all the rest by dorsal divisions.

Topographically the flexor surface is turned towards the body, the extensor surface away from the body; the flexor surface of the foot and the hand rest on the ground in locomotion. The extensor surface, being the less protected, is covered with a hard, leathery skin; the large arteries ran originally to the limb along the protected flexor surface. On the flexor aspect, particularly on the palm and sole, the epidermis becomes thickened and horny, forming pads, and the hair is lost, whilst on the extensor aspect the extremities of the digits form claws, hoofs and nails.

Para. 69. A deeper analysis of the structure of the limbs reveals their segmental origin.

In the extremities we see definite portions of the ventral parts of the trunk segments in a widely transplanted position. In the upper extremity there are included the fifth to the eighth cervical segments and the first thoracic; for the lower extremity the first lumbar to the third sacral (21st to 28th). The embryonic material that affords to these segments the primordia for the skeletal musculature, skin and nerves, does not remain separate segmentally, but is welded together to form new combinations, out of which the bones, muscles, nerves, skin and blood-vessels arise, as we are able to dissect them. This segmental fusion is shown by the events in development, by a comparison of the positions taken up in various animals, and through the analysis of the position in some particular form (as in man for example). For this analysis the nerve supply is the best criterion.

Let us ignore the difficulties of individual parts of the skeleton and look at the muscle (Bolk, in Rynbeck). These are [para. 67] no longer lower units (myotomes) but higher units (muscles), which have been derived from the fusion of few or many myotomes. Since at an early embryonic time, with the beginning of the somite, the segmental nerve connected with these, and since in the outgrowth of the limb bud the connection once developed is not lost, so the transformation of the myotome into muscle brought about the plexus formation of the nerves. Since further the limb bud arises from the ventral side of the trunk only, so the plexus is formed only of the anterior primary divisions of the nerves.

The scheme (fig. 33) shows how the middle segments in the upper limb become displaced outwards, the fourth forming the cranial, and the tenth segment the caudal boundary, and how in the lower extremity the caudal segments of the sacral plexus are situated behind and below, the upper segments above and in front.

The nerves of the upper extremity show throughout an arrangement typically in accord with this mode of origin. Of the two borders of the upper limb, along its ventral aspect, the one lies in the limb horizontally abducted and palm facing forwards cranially (on the thumb side), the other caudally (on the little finger side). The former is related to the cranial roots 5, 6, 7, and the other to the caudal roots 8 and 9. The dorsal surface is related serially to the roots 5 to 9. From the anterior surface there arises by fusion the median nerve, which therefore contains all the segments. The cranial margin is related to the musculo-cutaneous nerve, which comprises the fifth, sixth and seventh, whilst the caudal border is related to the ulna, which comprises the eighth and ninth segments. The former follows the radial border of the forearm, the latter the ulnar margin. The ventral roots innervate the flexor muscles [see para. 68 above] ; the dorsal divisions, the extensor muscles.

No fibres belonging to the cells of origin of the musculo-spiral nerve go to the muscles of the flexor surface ; if this occasionally should be the case (and it is not seldom the case in the brachialis muscle) more exact investigation shows that the nerves within the plexus have aberrantly pursued a different path.

In the region of the lumbo-sacral plexus conditions are somewhat different since more segments (10) are involved. The four upper segments (21 to 24) are found only on the extensor aspect of the thigh and along a strip on the medial side of the thigh (area of the saphenous nerve). The succeeding four segments (25 to 28) go to the flexor aspect of the leg, ankle, joint and foot. For the principles governing this arrangement see below.)

The segmental division of the muscles is as follows:—

Shoulder muscles	from 5th and 6th segments
M. biceps	
M. brachialis	
M. brachioradialis	
M. supinator	
M. coracobrachialis	5th, 6th and 7th segments
M. extensors of the forearm (radial group)	6th and 7th segments
Superficial flexors of the forearm	
M. triceps and remaining extensors of the forearm, also the opponens pollicis	6th, 7th and 8th segments
Remaining thumb muscles	7th and 8th segments
M. flexor sublimis and profundus	7th, 8th and 9th segments
M. pronator quadratus and remaining muscles of the hand	8th and 9th segments
Muscles of the lower extremity:—	
M. ileopsoas	22nd and 23rd segments (L. 2nd and 3rd)
M. sartorius	
M. adductores	22nd, 23rd and 24th segments (L. 2nd, 3rd and 4th)
M. quadriceps	
M. tensor fasciæ femoris	24th and 25th segments (L. 4th and 5th)
M. tibialis anterior	
Dorsal musculature of the foot	24th, 25th, 26th and 27th segments (L. 4th and 5th, S. 1 and 2)
Medial flexors of the ankle	
M. extensor hallucis	
M. ext. dig. longus	
M. biceps femoris	25th, 26th, 27th and 28th segments (L. 5 to S. 3)
Deep flexors of the leg	
M. triceps of the leg (gastrocnemius, soleus, plantaris)	
M. flexor hallucis, longus, and remaining foot muscles	25th, 26th, 27th and 28th segments (L. 5 to S. 3)

General topographical principles hold now only in so far as the more proximal muscles are supplied by higher segments and the distal by lower segments; and moreover the muscles on the extensor side of an extremity are supplied by lower segments than the flexor muscles at the same level.

The sensory branches follow a different principle in their distribution. In the upper extremity the area of the fifth, sixth, and seventh segments lies on the radial (thumb) side (the cranial border of the horizontally abducted arm, the palm facing upwards); the area of the eighth and ninth (dermatome) along the ulnar margin. The line of division between them runs on the flexor aspect to the fourth finger (3½ + 1½ fingers), on the extensor aspect to the third finger (2½ + 2½). In the lower extremity the dermatome of the 21st to 24th segments (plexus lumbalis) lies along the extensor aspect of the thigh, and along a strip stretching to the inner malleolus along the medial side of the leg (saphenous nerve). The lower dermatomes occupy the flexor aspect of the thigh and leg and also include the front of the leg.

It is to be observed that the areas of cutaneous innervation do not correspond with the dermatomes, but rather that in each skin area there are several segments. Destruction of several dorsal roots therefore only occasions a diminution of the sensibility of the skin and not complete anæsthesia of a skin area.

Also the arteries of the extremities in the beginning, as is shown by their development, start as several arteries.

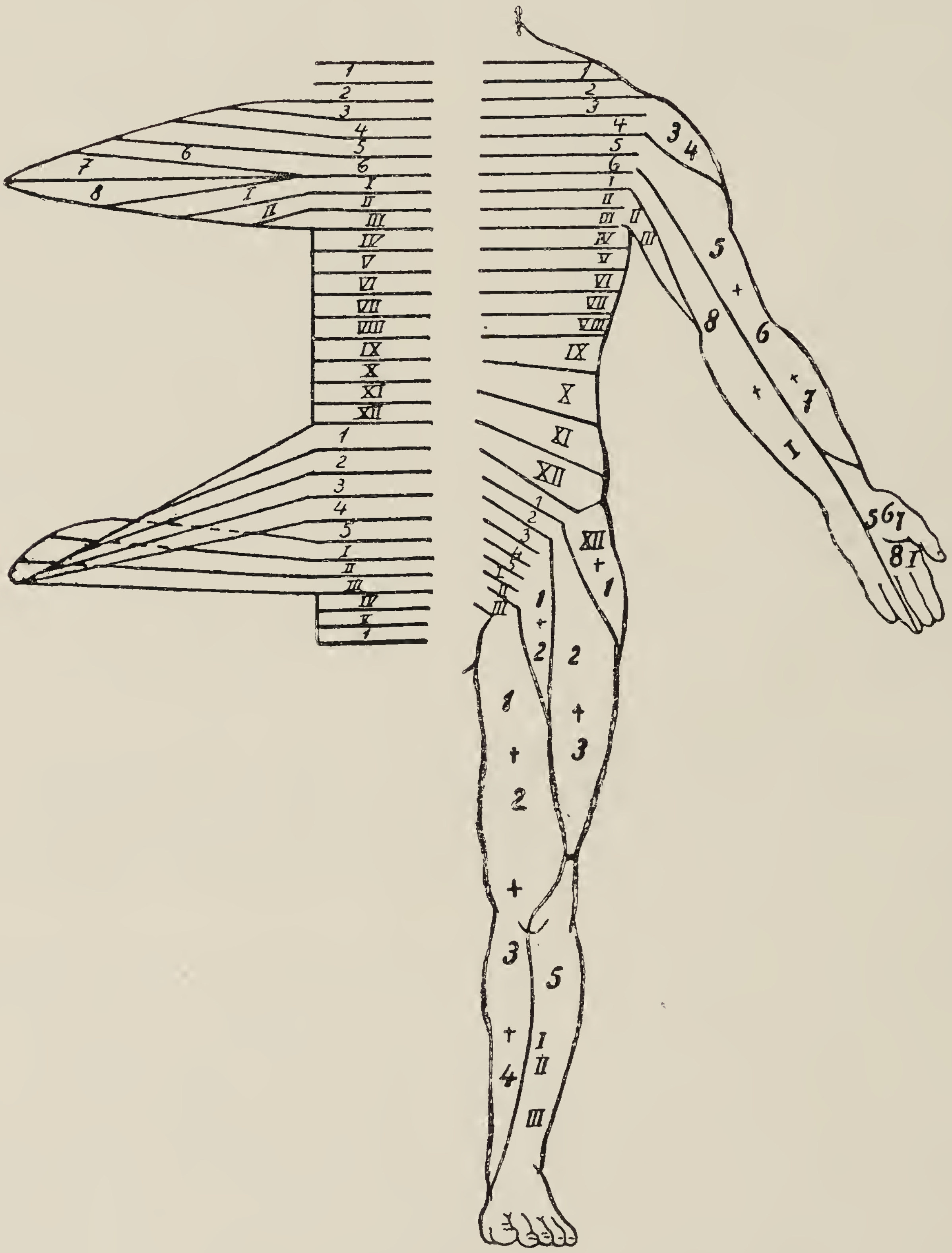

FIG. 33.—Scheme for the understanding of the segmental divisions of the body. (From Schultze-Lubosch, "Topographical Anatomy.")

According to some, these segmental vessels in the upper extremity are related to definite parts of the limb. One of these arteries attracts all the blood-stream, and this, of course, in the upper extremity is the seventh segmental, the subclavian, and in the lower extremity the 23rd or 24th the (4th or 5th lumbar artery) which is the sciatic or inferior gluteal. In both extremities, the vessels form a vascular net which surrounds the principal nerves. Out of this the remaining arteries are formed. The final arrangement is typical for the different orders of mammals.

In the upper extremity it is to be noted that the right and left subclavians are not of the same morphological value. Only the left is directly a segmental branch of the aorta (fig 31 accessory and principal figure), whilst on the right it includes the fourth aortic arch and a part of the dorsal aorta, and then becomes a segmental artery. The vessel then attains a typical relation to the brachial plexus which it traverses. Consequently the two heads of the median and the median nerve itself lie in front of the artery. It is especially important that there can arise from the vascular net surrounding the median nerve an artery which does not traverse the plexus, but lies in front of the brachial artery and is known as the anterior brachial. It is the principal vessel in many mammals. If it occurs in man it is to be regarded as atavistic.

In the lower extremity runs the sciatic or inferior gluteal artery. It is found as in the upper extremity along the flexor surface. It is the principal artery in reptiles and birds and is recapitulated during ontogeny in man. Preceded by well marked anastomoses, the femoral artery arises in the second month of fœtal life, on the extensor aspect, whilst the inferior gluteal undergoes reduction (Nauck). It persists, however, very often as that branch which accompanies the great sciatic nerve. When the femoral artery passes through the adductor canal it restores the original arrangement of the artery on the flexor surface.

Para. 70. Three fundamental questions relating to the morphology of the extremities remain to be answered in regard to their homologies (General Homology, p. 101). Two things make the answers difficult. The agreement in ground plan between the two extremities is seductive in that it induces one to find in the other extremity what is found in one. The different positions of the two limbs easily induce one to assume that a perfect homology can be established through the fictitious rotation of one or the other extremity. In reality, the fact is that the ground plan repeats itself as the typical vertebra and the ribs repeat themselves throughout the vertebral column.

No more than a lumbar vertebra, except in type, resembles a cervical vertebra, or the hyoid bone a posterior gill arch, can the extremities, notwithstanding the repetition of the type, be compared with each other in all points.

We see in the extremities side by side with the agreement in type differences clearly emphasized. The patella is an example of such.

The subdivision of the foot uses the material at its disposal quite differently from the hand. The thigh possesses in the adductors, the leg in the peroneal group, specific dorsal musculature which is absent from the arm; whilst the arm in pronators and the supinators possesses muscles peculiar to it. Flexor and extensor muscles are of course present above and below, but, between the triceps and the quadriceps, between the flexor muscles of the forearm and the flexors of the leg, there is no homology other than that of myotomic origin. Just as in the elements of the hand and foot so in the arm and the thigh the myotomic material is put to quite different uses. The flexor sublimis is absent from the leg. The triceps suræ has no counterpart in the forearm. There is no opponens for the great toe and the arrangement of the nerves is strikingly different. Flexor and extensor nerves, in the lower extremity, are fused into a single stem that traverses the flexor aspect of the limb, which is the same as if in the arm the ulna median and musculospiral were joined together into a single trunk. (The nervus maximus which indeed is found in the forelimb of the reptile.) The two principal nerves of the thigh cannot be directly compared with the principal nerves of the arm. These primary differences of the two extremities are to be looked on as something structural, which advances further through the different functions of the two limbs or in relation thereto.

A comparison between the upper and lower extremity is, however, valuable since, as we have said, the general type arrangement can be recognized despite the serial differences. Such a comparison is possible so long as one keeps in mind as a principle of the comparison the reposition of the limb in relation to the longitudinal axis of the body and its segmental relations. Where do the cranial segments lie in the arm and the leg? In the arm it is the cranial border which bears the thumb (the arm being abducted horizontally and the palm facing forward). In the leg it goes to the side of the great toe (position of the saphenous nerve which belongs to the lumbar plexus).

From this it follows that the tibia and the radius, the fibula and the ulna correspond to one another (cf. figs. 34 and 35 for the following). Moreover, the course of the nerves is important. In the upper extremity as in the lower a system of nerves passes in front of the girdle for the extremity (prozonal position, Bolk). In the upper extremity it is the greatest part of the whole of the brachial plexus, in the lower extremity only the femoral nerve. In the lower extremity the obturator passes through the pelvic girdle (diazonal, Bolk) whilst the sciatic passes behind the pelvic girdle to the extremity (metazonal, Bolk).

In the upper extremity we have only a few nerves in the diazonal position (nervus suprascapular). Above as below, the nerves destined for the flexor aspect remain in that position, whilst those destined for the extensor aspect wind around the caudal border of the limb. Above the musculospiral does this. It passes from the medial side to the lateral, behind the humerus and at the elbow-joint reaches the radium (sulcus nervi radialis). Below it is the peroneal nerve which passes around the head of the fibula to the extensor side.

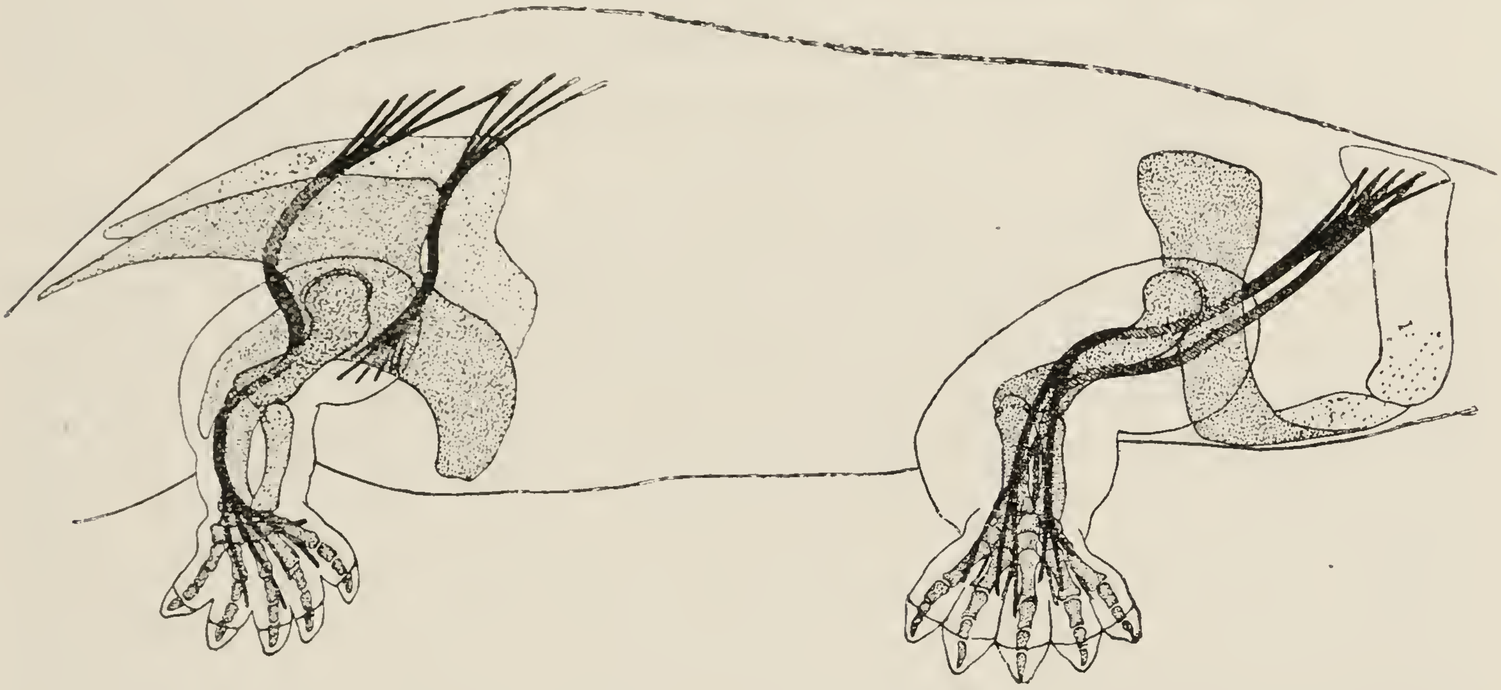

Fig. 34.—Primitive position of the extremities; skeleton schematically indicated in the outline of the body of a crocodile. The brachial plexus and lumbosacral schematically indicated. The nerves of the flexor surface of the anterior extremity clearer.

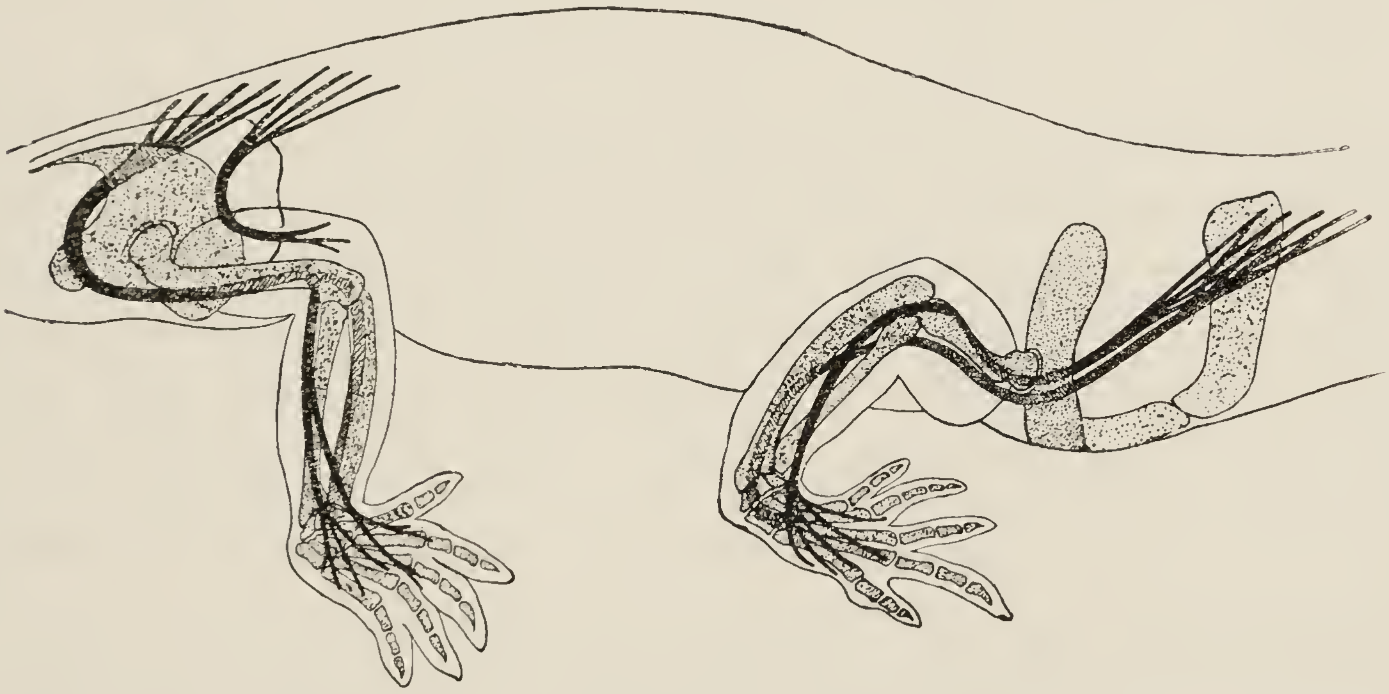

Fig. 35.—Secondary position of the extremities. Skeleton schematically drawn in from the body form of a lizard. Nerves of the flexor surface clearer.

The comparison cannot be perfect because the extensor of the leg is not of the same value as that of the arm from a segmental view. Through the prozonal femoral nerve and the diazonal obturator nerve the extensor surface receives nerves of a higher segmental level (lumbar plexus), as already mentioned. The comparison would be perfect if either the peroneal nerve passed to the front in the upper third of the thigh to the extensor region in front of the saphenous (which it does not), or if the musculospiral, the median and the ulna in one thick bundle comparable to the sciatic passed as far as the elbow-joint and then turned round the ulna border to the extensor aspect (so developed in the reptiles). This comparison shows that the ulna corresponds to the fibula.

An insight into the general principles of the two extremities is made difficult by their different relations to the transverse axis of the body.

If one goes back to the primitive position the contradiction is lessened (urodeles, amphibians, sphenodon, crocodile), although an ancestral form, in which both extremities have exactly the same relation to the transverse axis of the body, is in no wise realized. In such a hypothetical ancestral form (fig. 34) the stelepodium stands perpendicular to the trunk. At the elbow- and knee-joint the stelepodium is flexed to a right angle on the zeugopodium. The extensor surface looks upwards and outwards, the flexor surface downwards and inwards. The basipodium is bent at a right angle to the zeugopodium and the flexor surface rests on the ground. Radius and thumb, tibia and great toe lie on the cranial side; ulna and fibula, little finger and little toe lie on the caudal side. The nerves destined for the extensor surface cross from the flexor surface around the caudal border cranially on to the extensor surface.

In this position the extremities are only accessory organs of locomotion, locomotion in the main depending on the trunk musculature and the tail (Maurer and Nauck) (creeping and wriggling). The changed position first arises when the extremities become the bearers of the body raised above the ground. Then the stelepodia stand no longer in the transverse axis of the body, but in the longitudinal axis along the side of the trunk (fig. 35). The knee is turned towards the front, the elbow towards the back. The development of this position from the original one is clear in the case of the hind extremity, for if the knee is directed forwards then the toes can remain on the ground directed forward. In the fore-limbs this, however, is only possible if at the same time the head of the radius persists in an external position and its shaft crosses the ulna and its distal extremity lies internally to the ulna on the ground (pronation). In this position at all events the palm of the hand is found on the ground with the fingers directed forwards.

In man this pronation is yet visible in that the long axis of the humerus is twisted in the direction of the pronation of the fore-limb (torsion of the humerus). This torsion corresponds with the direction of the musculospiral nerve which arises for the reasons already mentioned, and makes the position yet clearer. The course of the musculospiral persists, however, in the absence of this torsion; it only prolongs the course of the nerve (Braus). The torsion of the humerus carries the upper limb in such a way that in man the resting position is already clearly pronated without sharing the pronation in the elbow-joint, and the thumb looks towards the front and the palm of the hand medially.

(E) Morphology of the Cavities of the Human Body.

Para. 71. The continuity of the organs of the body is broken many times through division and cavity formation (joint cavities, spaces in the connective tissue around the larger blood-vessels and organs, as for example, in the mediastinum, in the subperitoneal space of the pelvis minor, inguinal canal, or in the neck in the region of the pharynx, the anterior and posterior chambers of the eye). Other forms are such cavities as the mouth, the nose, conjunctival sac, ventricles of the brain, central canal of the spinal cord, lumen of the gut and, above all, the peritoneal sac and its subdivisions.

An attempt (O. Schultze) has been made to classify all these cavity formations into clefts and spaces. If there be an epithelial lining then the term cavity is applicable; if there is no epithelial lining then the term cleft is applicable. One has also to distinguish between true and false surfaces. This would approximately correspond to the previous separation. A true surface should be referable to the germ layer from which it was derived, whereas a false surface would be a secondary formation. Such limitations occasion great difficulty. The anterior chamber of the eye is a typical cleft space but is lined throughout with epithelium. The peritoneal cavity arises in amphioxus clearly in relation with the original gut cavity, but in higher forms it arises as a cleft formation. A coherent classification is not possible in existing animals.

Here we will only attempt a valuation from the morphological standpoint of those spaces which arise as part of the cœlomic cavity. In primitive conditions the cœlomic space is a single space which surrounds the gut on all sides. It ends behind the gill region. The pericardium is situated in it right at the caudal end of the gill region. This represents a closed space which originally was continuous cranially with the general cœlomic cavity and now contains the heart. It previously joined with the head cœlom (fig. 21). When a neck is formed the heart comes to lie in the front of the thorax and, laterally and behind, two recesses of the cœlom contain the lungs (amphibia, reptiles and birds). In mammals, through the development of the diaphragm, this recess becomes separated as the paired pleural cavities from the unpaired peritoneal cavities. Thus there are four serous cavities present. In addition to these there are the serous spaces around the testicles which originally were continuous with the peritoneal cavities. The relation of these cavities to one another is given in fig. 36.

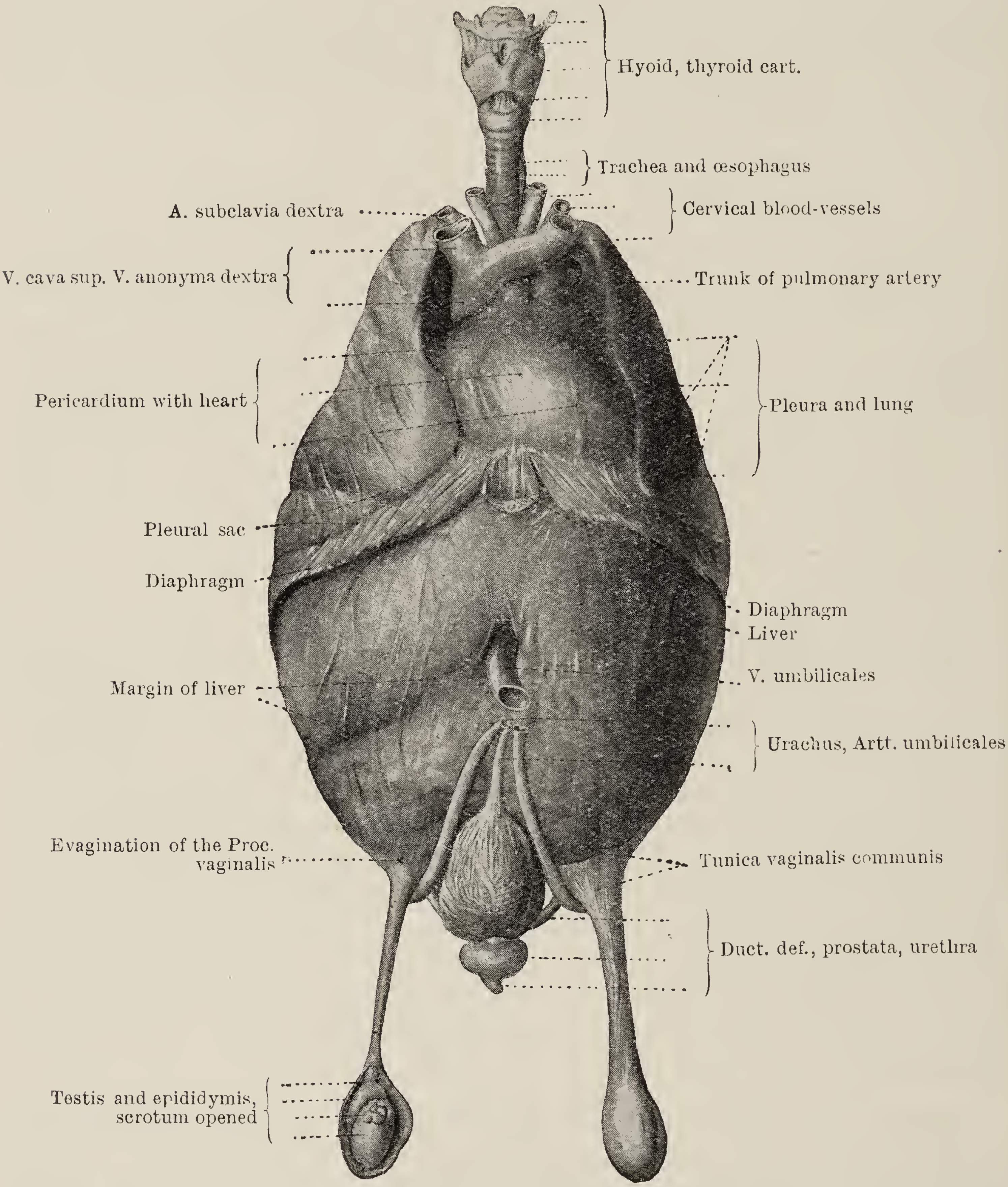
Hyoid, thyroid cart.
Trachea and œsophagus
A. subclavia dextra
Cervical blood-vessels
V. cava sup. V. anonyma dextra
Trunk of pulmonary artery
Pericardium with heart
Pleura and lung
Pleural sac
Diaphragm
Diaphragm
Liver
Margin of liver
V. umbilicales
Urachus, Artt. umbilicales
Evagination of the Proc. vaginalis
Tunica vaginalis communis
Duct. def., prostata, urethra
Testis and epididymis, scrotum opened

FIG. 36.—The divisions of the cœlom in a new-born child. The whole body wall removed. Original preparation figured in Schultze-Lubosch, "Topographical Anatomy," J. F. Lehmann, 1922, fig. 197. Reduced in reproduction about five-twelfths.

The serous cavities are not wide, open spaces, but everywhere of capillary dimensions. The walls of the contents and of the serous space glide on one another by means of reflecting surfaces wetted with serum. The reflecting surface is due to the covering of serous epithelium. The serum transudes from the blood-vessels of the serous membrane, which also posesses lymph spaces for the removal of the serum. The peritoneum as an organ, neglecting the purpose of slinging the gut, possesses two important functions ; above all, it is an excretory organ and also the source of the gonads whose ripe products it conducts to the exterior. Under primitive conditions, in the invertebrates and also in amphioxus, the cyclostomes and some bony fishes, there are formed no excretory ducts for the genital products. In the female sexual organs in all animals, including man, the egg ova are first shed into the peritoneal cavity and then transferred to the Müllerian duct.

The excretory organs are in the first instance canals, which pass from each segment to the surface of the body (nephridia, cf. fig. 11). The primitive form of the collecting duct joining these nephridia is not known to us (primary kidney or pronephros—pronephric duct). A likely hypothesis (Boveri) suggests that such a canal was originally a ridge on the surface of the body (fig. 12, a) and received the individual nephridia. Later it sank beneath the surface of the body. By this hypothesis one would be able to explain the observation that the pronephros and the pronephric duct arise from the ectoderm (Gegenbaur). The nephridial canals open themselves by means of nephrostomata into the peritoneal cavity (figs. 10, 11, 12). The organs developed from it, the pronephros and the mesonephros, in consequence, lie retroperitoneally.

The formation of the peritoneal cavity is enshrouded in darkness, and observations on vertebrates have contributed nothing to dispel the darkness. Early in the invertebrates an extensive cœlom is found, but there are two different forms of cœlom to be observed in these. They may be distinguished as primary and secondary. The primary is one where the space arises as a cleft between the ectoderm and the entoderm or by splitting in the mesoderm (E. H. Ziegler). It is therefore known as schizocœl (Huxley) (for example, in the sponges). This division is naturally to be referred back in the last resort to the formation of the blastula cavity. The secondary peritoneal cavity on the contrary arises in a large series of invertebrates (e.g. echinoderms, enteropneuts, balanoglossus and chætognates) who accordingly form the peritoneal cavity originally segmentally arranged by constricting off small sacs from the primitive gut. Particularly striking is the agreement which has always been observed in the formation of these peritoneal diverticula between the chætognates (sagitta) and the most primitive vertebrate (amphioxus). All these forms of the cœlom have been known as enterocœles, its possessors as enterocœliers (O. and R. Hertwig). In other forms, however, the cœlom arises without this relation to the entoderm, and of course as a series of spaces segmentally arranged which arise within the mesoderm. Platodes and nematodes (fig. 11, on the right). In the changes of the cavity arise the sex cells, so that this form of peritoneal cavity may be described as "gonocœle" (Hatschek, Meyer, Rabl). The question is now, if the peritoneal cavity arose originally in the form of an enterocœle or as a gonocœle? The enterocœle theory suggests that the peritoneal cavity may be referred back in its ancestral form to a diverticulum of the primitive gut, which has possessed nutritive function and at the same time has furnished the developmental material for the sexual elements (Haeckel). The peritoneal cavity would have its original form approximating to the canal system which runs as a vascular system in the medusa (cœlenterates) from the primitive gut to the body (gastro-vascular system). The findings in balanoglossus, sagitta and amphioxus (cf. Korschelt and Heider, figs. 183, 185, 189, 192), according to this theory, ought to display a repetition of this primitive development. The establishment of the cœlom ought to present a division in the mesoderm (nematodes and higher secondary vertebrates) concealed by the rich possession of yolk that arises. The enterocœle finally includes the vascular circulation. Blood-vessels and blood-cells arise demonstrably in many cases from the entoderm. By a change in position during development these cells can be displaced into the mesenchyme. In the widest sense the vascular system might be compared to a differentiated hollow system derived from the cœlomic cavity.

On the contrary, the gonocœle theory suggests that the segmentally arranged cœlomic cavities began as a series of cysts for the sexual elements (fig. 11, on the right); it may then have fused into a single cavity; the development of the cœlom from the primitive gut might be regarded as a distinct process. We have already considered this theory in regard to the origin of the metameres.

Each of the two theories has its justification, each might satisfy the other, in so far as the formation of the cœlom is related, under all conditions with the middle germ layer. The mode of formation of the middle germ layer is favourable to both theories.

If we suppose that the multiplying material which represents the formative cells of the middle germ-layer undergoes many displacements of the material, right up to the time when the layer is formed, this affords the possibility of explaining each theory from the standpoint of the other. In the main stem of the dividing cells one encounters in the invertebrate a stage when a definite cell group forms the stem group for the entoderm and mesoderm. This group by division gives rise to both mesoderm and entoderm. In this form, which serves as the base of the gonocœle theory, the primitive mesoderm cell is the mother of all, later the segmental cœlomic cavities including mesoderm. The enterocœle theory could insist that in these cases the mesoderm and along with it the cœlomic cavity arises from the entoderm. This derivation, however, is passed through at the earliest stages of development, and when the entoderm is formed the origin of mesoderm from it is no longer to be observed. On the contrary, however, the gonocœle theory can insist that the derivation of mesoderm from the wall of the archenteron is only of apparent value, since it represents only the displacement of mesodermal material into the wall of the archenteron during development. The fact that in the vertebrates mesodermal material can be proved to exist at the blastula stage and can be proved to arise in two places (gastric and peristomal mesoderm) is not favourable to this opinion. In respect to the germ cells we now know that they are certainly not derived from the germ layers, but they are cells which can be referred back to one of the two first cell divisions immediately following fertilization. They therefore do not arise in a germ layer (mesoderm) but first exhibit themselves through changes in this layer. There is no germ epithelium in this sense—it is only the place in which the germ cells begin and perfect their development.

From the development of the germ cells neither theory can draw anything of value to it.

Finally, one has made allowance for the possibility that in the metazoa the formation of the cœlom need not be referred back absolutely to a single plan. This would be acceptable if in vertebrates both types were not found in forms closely related. Amphioxus shows the pure enterocœle formation; the remaining vertebrates, on the contrary, the division of mesoderm. It is scarcely to be believed that in the chordate stem the cœlomic cavity is not throughout a homologous structure.

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(II) Morphogenesis of Man

Para. 72. We have already remarked that morphogenesis must form the further subject matter of this work, and we have discussed the standpoint from which this should proceed [para. 40]. It must include particularly the general and special morphology. Since, however, the latter (special embryology of the organs), without at the same time referring to the comparative anatomy of the organs, is not scientifically possible, we shall neglect this aspect (cf. Foreword). Our presentation of the morphogenesis therefore only includes the general embryology up to the stage of the completion of the "neurula"—that form of the metazoan body in which the primitive organs are laid down. Our presentation will show that in the development of this primitive form there is followed a definite architectural plan.

It will show that the ancestral primordium, in order to develop along this definite plan, and together with the necessity of forming its manifold developmental systems, behaves in a remarkable manner. The developmental processes of the mammalian, and especially the human, egg are not wholly or easily understood. For the scientific understanding of the human ovum we must consider before all that, in order to achieve its purpose, it must start from the necessary conditions. The neurula is a very simply organized ground form. A longitudinal body contains the primitive organs (neural tube, chorda, primitive vertebra, gut); symmetry and segmentation are easily seen. Organ formation is only just beginning. So morphogenesis as we have defined it here will include our earlier presentation [para. 54]. We must assume a knowledge of embryology, at least of its groundwork.

According to the earlier considerations [paras. 9, 35] we will describe not only the "how" of development and the formula it follows, but also consider the conditions of structure formation; that is, the "why" of the ontogenetic processes will be investigated and the applicability of the rules and laws be critically examined. A third final portion will attempt to make clear the inner method of the developmental process and its peculiar driving power.

(A) Formative Processes.

(1) Fundamental Processes of Primitive Development in Non-mammalian Forms and the Theoretical Questions thus raised.

(a) Formation of Primitive Organs.

We assume the knowledge of the formation of the ovum itself, and its various types, as well as the formation of the blastula, as we meet it in amphioxus and in the amphibia, and begin our survey at the point where we meet the gastrulation process in the egg of amphioxus. The formation of the gastrula begins here as an invagination. This (figs. 37, B, C) so perfects itself that it engulfs the vegetative material. This material in consequence of the rotation of the fertilized egg is directed behind and above. The blastopore which thus arises is first wide and then shuts itself eccentrically.

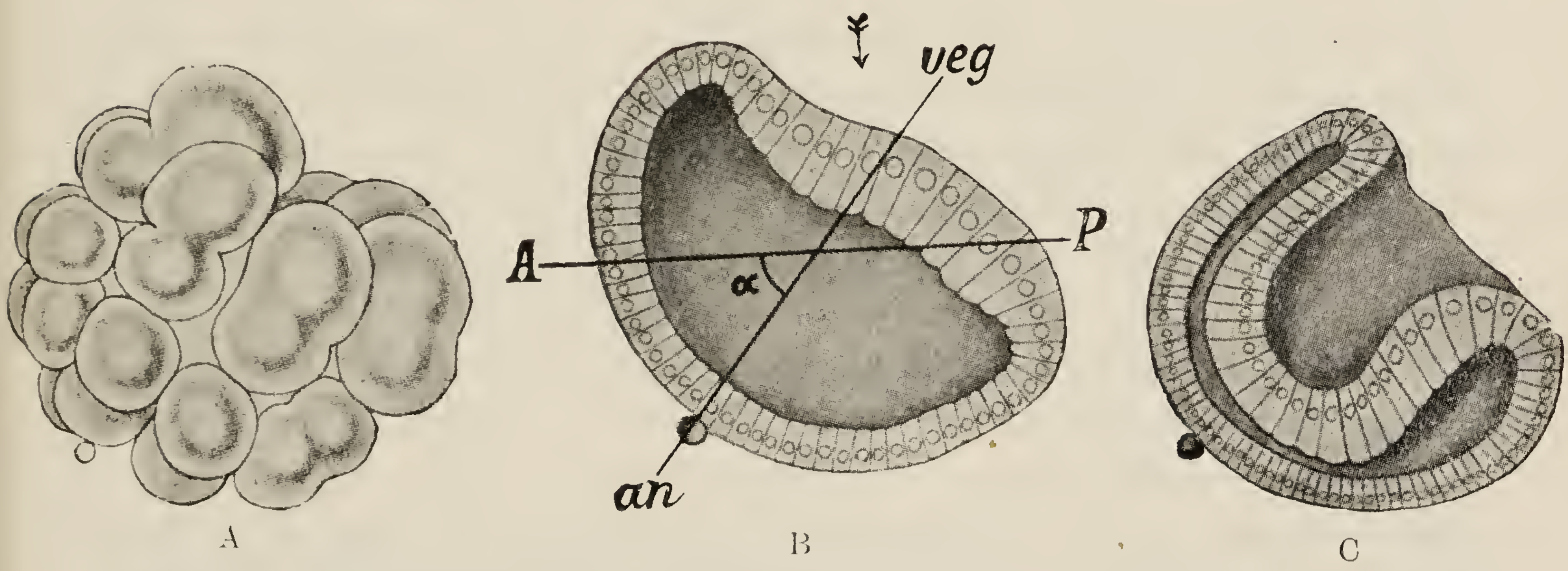

Fig. 37.—Three stages in the development of Amphioxus after Cerfontaine from O. Veit, Ergeb. d. Anat., Bd. 24, 1923. A, segmentation stage; the embryo is bilaterally symmetrical and shows the animal pole (position of the direction granule below and to the left) rotated. B, wide blastapore lying on the aboral side; beginning of invagination. Axis of the egg (between direction granule and middle of the blastapore, animal and vegetative pole) and embryonic axis (cranio-caudal) do not coincide. A = anterior. P = posterior. C, progressive invagination, which advances towards the interior of the cells of the animal area on the dorsal surface.

This happens in such a way that the animal pole becomes the blastopore and the vegetative pole either remains the same or diminishes. Through this change the interval between the animal pole and the blastopore forms the dorsal surface of the animal. Through swelling and displacement of the cells they become pressed together in the middle line. At the same time material from the margins of the blastopore is displaced inwards but also dorsally so that the entoderm arises not only from the vegetative cells originally present and which are situated along the ventral surface (fig. 37, C), but in addition from cell material which was originally at the animal pole. The rotation of the whole egg which brings the animal pole, originally directed upwards, downwards and forwards, is already completed in amphioxus after fertilization owing to the enclosure of the egg protoplasm. The axis of the egg between the animal pole and the vegetative pole does not coincide with the axis that joins the oral and aboral pole of the animal (embryonic axis figs. 37, A, B). The formation of the embryonic organs begins in the dorsal surface when formed after the completion of gastrulation.

Para. 73. Increase of yolk confuses the clearness of the structure. The contrast between the actively dividing animal cells and the heavily laden huge vegetative cells is striking. The liveliest cell growth is now found more between the animal pole and the last invaginated point (the latest aboral pole). So there arises outwardly a typical displacement of the processes, at the same time difficult to follow in time. The process of gastrulation is displaced backwards in the process of division (fish and amphibia). The invagination process begins in the neighbourhood of the vegetative pole between this and the posterior pole of the embryonic axis (fig. 38, *a*). The large vegetative cells do not allow of an invagination. The segmentation cavity is only pushed lengthwise and the archenteron is enlarged accordingly, so that the mobile material on the animal side is easily displaced in the direction of the arrow (fig. 38, *b*) around the lip of the blastopore and further lengthened in front (fig. 38, *c*), quite like therefore the corresponding process in amphioxus. But also, and this is a difference, the animal material on the other side of the egg is displaced forwards (fig. 38, *c*). The final gastrula is here a product of invagination and protracted segmentation. Whilst a blastula appears black above and clear below, the completed gastrula appears quite dark, because the opaque material reaches it from all sides and the clear material forms then only a sharply bounded white plug (yolk plug). The blastopore (the black margin) is not open but is closed by this plug (fig. 38, c). A change and displacement of the centre of gravity arise here. The dorsal surface looks upwards, the ventral surface downwards, the embryonal axis cuts the oral and aboral poles. The animal pole here appears to remain above while earlier it had the same position as in amphioxus (fig. 37, *b*), at least this is given most recently for the gastrula of triton (Vogt). In such cases, the embryonic form would be produced, not by rotation, but by the more general disposition of the mass. These processes cannot be referred back to any generally valid principles.

However this may be, it is important that in amphibian eggs an elongation of the later dorsal surface, which is formed by cell proliferation and stretching, appears to be connected with the displacement of material from the front to the back and around the lips of the blastopore, and is again found towards the front (fig. 38, *c*, direction of the arrow).

An association, however, arises between these forms and amphioxus which also embraces all the non-amniotes. In all there arises a time interval between gastrulation and the starting of the process of organ formation. The latter first begins when gastrulation is complete. How it proceeds the following models attempt to demonstrate (fig. 39). Right in front of the dorsal lip of the blastopore (from where the tail bud will develop backwards) the cell material of the whole area is collected. Along the heaped-up margin the ectoderm is transformed into entoderm, and from the margin the middle germ layer arises (for this reason called the peristomal mesoderm). Further towards the front this special material is divided into four organs: the medullary plate, the chorda, roof of the permanent gut and the mesoderm. The neural tube is free in the widest part behind. Beneath it the chorda is released from the roof of the primitive gut, along its lateral border the mesoderm arises (here therefore called the gastral mesoderm). The whole process, very like that in amphioxus, is known and often pictured.

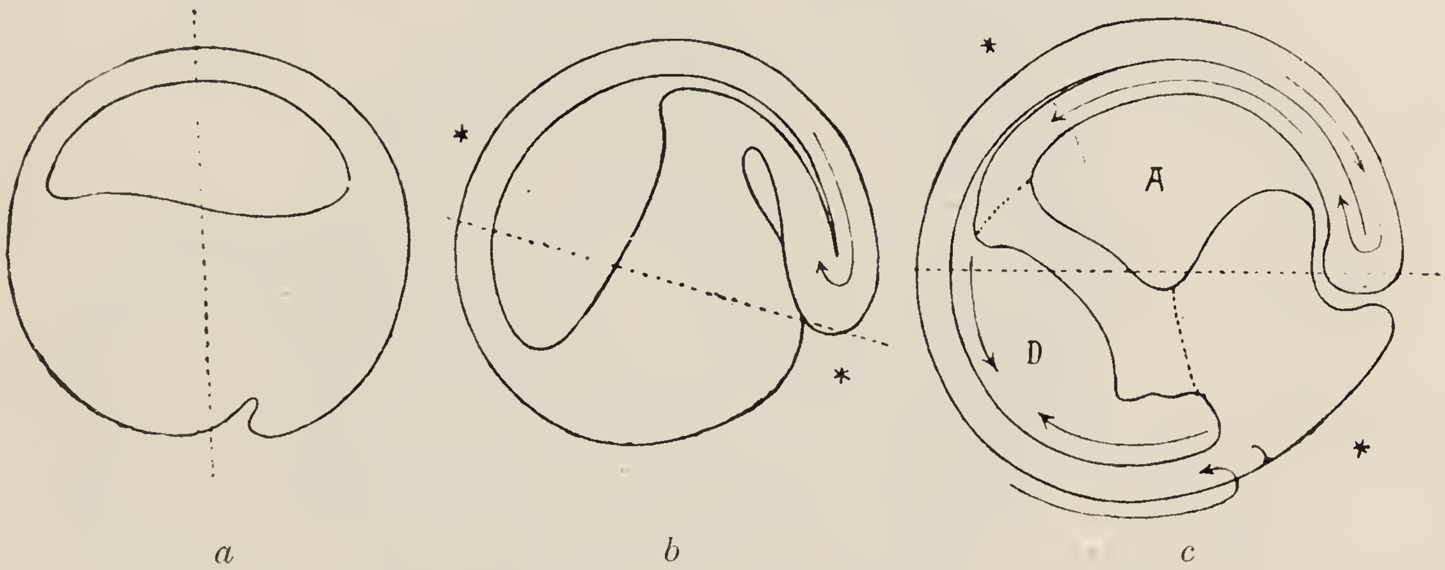

Fig. 38.—Three stages in the gastrulation of the frog; the drawing of the outlines of *b* and *c* are based on the wax reconstructions of Eckstein; *a*, from a picture by O. Schultze in Hertwig's "Textbook." The dotted line in *b* and *c* is the embryonic axis. The asterisks in *b* and *c* indicate the position of the animal and vegetative poles (egg axis). In *a* the embryonic and egg axes coincide. Further detail in the text.

It is to be regarded as a continuous differentiation from the front to the back (that is, the youngest part lies behind [p. 190]. Behind there is increment, displacement of material to the blastopore and indifference hand-in-hand (figs. 38, *b*, *c*). The spot, which in figure 39 indicates the collection, would, in further development, take on the forms which now occupy the anterior part. It is especially important to recall the points of origin of the mesoderm, which are not accidental but already in the vertebrates and in amphioxus play an important rôle, and are therefore fundamental in the organization of the metazoa [para. 71]. Both mesodermal areas differ not fundamentally but only topographically and in respect to their formative material from one another. In the beginning a part springs from the roof of the archenteron and a part from the region of the blastopore. However, the blastopore will form the embryonic area and here the peristomal mesoderm becomes gastral mesoderm. The peristomal mesoderm becomes of significance, since in the amniotes where its place of formation lies outside the embryo it becomes the source of the extra-embryonic mesoderm (p. 290).

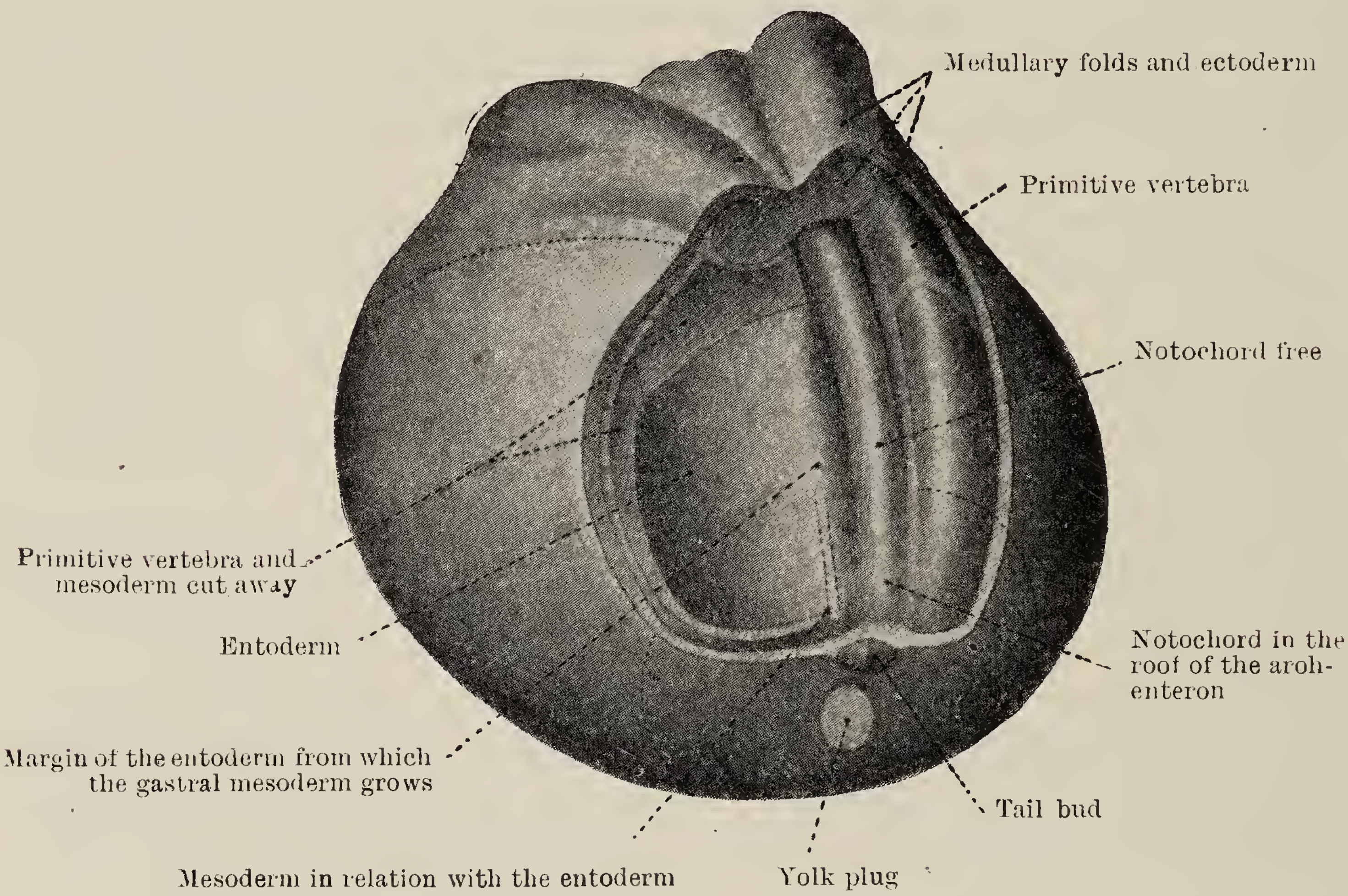
Medullary folds and ectoderm
Primitive vertebra
Notochord free
Primitive vertebra and mesoderm cut away
Entoderm
Notochord in the roof of the archenteron
Margin of the entoderm from which the gastral mesoderm grows
Tail bud
Mesoderm in relation with the entoderm
Yolk plug

FIG. 39.—Schematic representation of the axial organs of a frog's neurula. Based on a wax model of the Ziegler's series, enlarged about three times. The ectoderm behind the primordium of the brain and in front of the tail bud is to be imagined as cut away, so that the wall of the gut (that is here, where no mesenchyme is developed, entoderm) is visible.

By the formation of the chief of these four organs, namely, the central nervous system, one reaches that embryonic form which, arising after the gastrula, possesses these four organs and is described as the neurula.

Independent of the formation of this organ the development of the brain follows. This arises in the neighbourhood of the animal pole (before it?). Consequently two regions differentiate themselves in the embryonic head and trunk regions. If head formation (cephalogenesis) and trunk formation (notogenesis) are really quite sharply separated from one another, or if one had better speak of an anterior and posterior head region (Holmdahl), it is hard to say. It is certain that the anterior region arises in loco from existing fully differentiated material and grows backwards from there. The posterior part is formed from indifferent material which has first to be produced by proliferation. The special events, for example, the formation of the ventral mesodermal area, will here not be traversed, for we are concerned only with the elucidation of the gastrulation and embryo formation (neurulation).

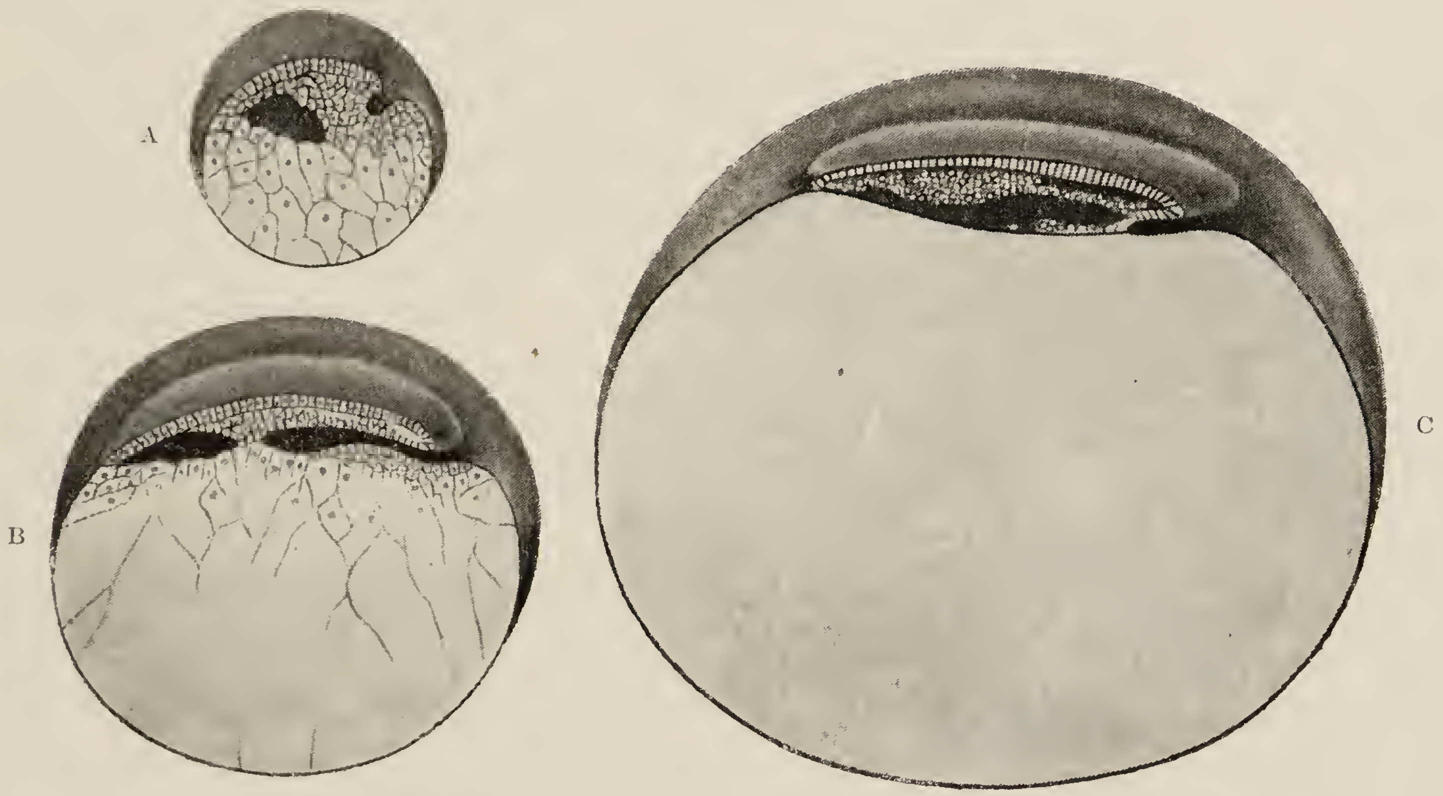

Fig. 40.—Gastrulæ of Petromyzon (Cyclostome, on the left above), Chimæra monstrosa (Holocephaly on the left below), Selachian (on the right); from O. Veit, l. c. The gastrula of Petromyzon shows segmentation cavity and archenteron (also to the front), and deutenteron, i.e., the cænogenetic entoderm. Further detail in the text. The sections drawn in the original figures are here reproduced plastically.

Fundamentally the process proceeds quite similarly in the meroblastic fishes (fig. 40, A, B, C). Both (figs. 40, B, 40, C) figures show beside the gastrulation of a petromyzon larva (fig. 40, A) a true archenteron, whose primordium (fig. 40, C) naturally runs spherically around the whole germ but laterally and in front remains without morphological influence, since the embryo is already formed before the inclusion of the yolk, which here is necessary, is complete. This surrounding growth is at all events a protracted segmentation. The embryonic formation invaginates temporarily the segmentation cavity but can be separated, as in the previously mentioned forms, since—at least at the site of the embryonic formation—gastrulation is concluded when the neurulation begins. Here, also, the head formation is independent of the trunk and tail formation. Trunk and posterior part of the body arise through a differentiation which starts in front from the indifferent material of the dorsal lip of the blastopore (that is, in front it first becomes visible (Rückert). Here also it forms peristomal (marginal) and gastral mesoderm. The transverse segmentation of the ground plan of the vertebrate body formation is here unrecognizable. Only a more essential difference arises which, in amphibia, at least in its effects, is altogether of the same kind (fig. 38, *c*). This is that the primitive archenteron (frog) is occasionally so represented that the cell material (fig. 38, *c*) between the stippled line separating the segmentation cavity and the archenteron fuses and disappears and the two (D) cavities on (A) become continuous. Then the entoderm grows in the dirction of the arrow along the roof of the segmentation cavity in order to meet the oral pole. Since a greater part of the entoderm is only prolonged through the displacement of cells dorsally, this continuous cell displacement establishes nothing fundamentally new. This formation of the archenteron is found regularly in the meroblastic fishes (fig. 40, *c*). A perfect invagination is not possible here since the second cell layer is displaced under the first by the invaginated material (40, *c*) as well as by the surface of the yolk (yolk syncytium). In order to make clear these formations, special drawings have been made, and these we must refer to. One distinguishes the primitive gut arising by invagination as the archenteron (fig. 38, *c*, A), that brought about by the segmentation cavity as the "deutenteron" (fig. 38, *c*, D), the two areas of entoderm as the palingenetic and cænogenetic entoderm p. 322.)

Para. 74. In the amniote egg now arises the further complication that not only is gastrulation temporally displaced into the stage of segmentation but also neurulation into the stage of gastrulation. Apparently this happens in quite different embryonic forms. The whole series, however, is architecturally quite clear. The immobile yolk is a factor that intervenes in place of the mobile vegetative cell material. Also the germ layer of the reptiles and birds is differentiated polarly, exactly as the gastrula of the anamniote, and displays an embryonic axis from in front and behind, and right and left. Also, the dominating growth lies behind. At this point there is found a true invagination (reptiles, most birds, only very obscure in the chick, many mammals, very clear in man [p. 288]. The yolk hillock can only become incorporated in the growing embryo, as in fishes, through the surrounding growth. This therefore causes the segmentation cavity to continue at the margin, gradually covering the yolk with the ectoderm and the entoderm like a cap (fig. 42).

Since the various sizes of the cells of the morula and the difference between segmented and unsegmented eggs, in the last resort, depend on the polar differentiation of the eggs, the dissimilar behaviour of segmentation and gastrulation is only an index of the different working out of the polar differentiation of the cell (Fuchs).

In the primitive gut of the amniotes one distinguishes fundamentally an archenteron and a deutenteron, and the palingenetic and cænogenetic entoderm, both of which form the roof of the primitive gut (entoderm), and from consequential folding of the embryo form the gut: the schema (fig. 41) elucidates the steps.

We may follow without further ado the frog gastrula, remembering that the yolk is very small. Unfortunately the much-investigated chick shows no archenteron and no palingenetic entoderm. Here the whole of the primitive gut is archenteron and the whole entoderm cænogenetic. The great service of Rauber is to have recognized this double-layered germ sheet of the chick as the gastrula.

Things are much more difficult in the comparison of the neurula. The formation of the neurula is completed, as mentioned earlier, during the formation of the archenteron. The process starts at the same time as this formation, and in the amphibian egg first begins after the stage of figure 38, *c* is perfectly complete. The formation of the embryo is the consequence of a differentiation which passes from the front to the back. It includes a previous determination of the cells proceeding in the same direction [para. 85]. The cells, of the dorsal axis are to be regarded, from the front to the back, as a graduated differentiation area. In the amniotes this graduation exists too, though it appears that determination of the cells and the starting point of differentiation occur at a much earlier time (at the earliest in mammals, p. 290). Each time we see that the neural tube, the chorda and the mesoderm are formed from the dorsal margin of the blastopore during the invagination. For the formal understanding the deciding question is now where the blastopore of this embryonic form lies. Then, if a formal agreement is present, we must expect that the germ layers should fuse at the margins of the blastopore, and that in front of the blastopore the separation of the axial organs from one another should occur.

Where then lies the blastopore? It is to be sought in the primitive streak of birds and mammals (primitive groove of reptiles).

A scheme (fig. 42, left and right) elucidates this exposition. If one imagines that the blastopore is extended longitudinally and that its borders become prominent one then has the primitive streak. Its dorsal lip is the primitive knot. The primitive folds are the lateral lips of the blastopore. The difference between it and the blastopore of the anamniotes lies in this, that in the amniotes the surrounding growth reaches only the blastopore, while in the sauropsida the growth is quite independent of the blastopore and the final end of the surrounding growth is in a quite

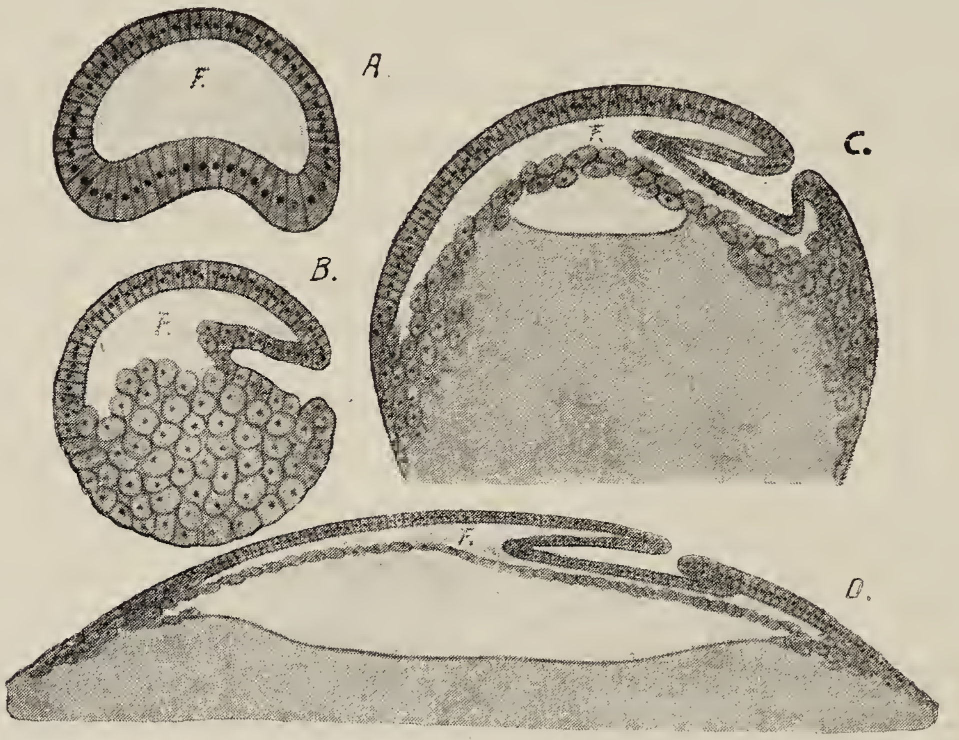

Fig. 41.—Picture of the cænogenetic entoderm in the hypothesis of Wenkebach (Anat. Anz., Bd. 6). *A*, amphioxus, *B*, cyclostomes and amphibia (cf. figs. 38 and 40). *D*, reptiles. *C* is a hypothetical stage. The capital *F* in the figure indicates the segmentation cavity. It becomes in *D* the deutenteron in which the advancing layers of epithelium break through into the archenteron as is shown in fig. 38c. Original figure reduced by four-fifths.

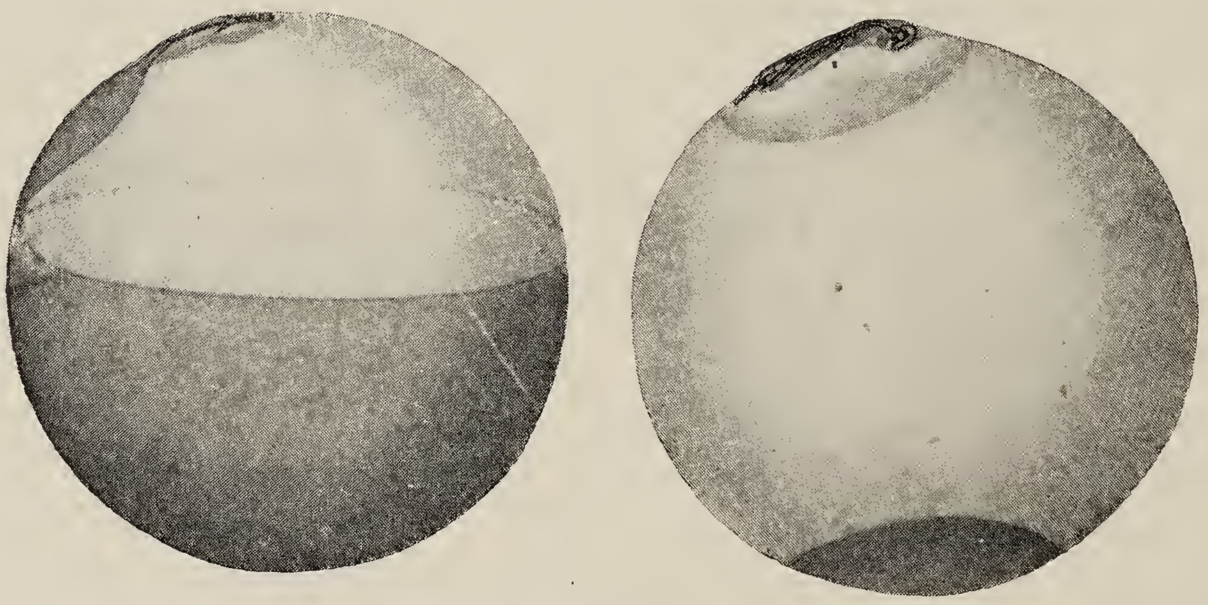

Fig. 42.—On the left the relation of the primitive streak and blastopore in Rauber's theory. On the right, chick on the germinal disc, the latter on the egg-yolk. The proportions of the embryo to the egg-yolk too great. The shaded area in both figures is the egg-yolk as yet unenclosed by extra-embryonic ecto-, meso- and entoderm; on the right below the yolk blastopore.

different place, the so-called yolk blastopore. In this difference between the marginal state and the central state of the embryo a fundamental thing in the primitive development of the vertebrate embryo has long been recognized. This is, however, no longer possible when one has recognized in the bony fishes an independent surrounding development growth of the egg yolk after the closure of the blastopore, a development of the embryo which is not marginal. If the primitive streak is the blastopore there must in the knot (the dorsal lip of the blastopore) be present a relationship of all three layers, and mesoderm must grow out from the lateral margins of the blastopore (the primitive folds) (peristomal mesoderm). This is actually the case. Further the position of the invagination must always be found immediately behind the dorsal lip of the blastopore. This is also the case. Finally the dorsal surface of the embryo and the axial line of the organs must arise always in front of the primitive streak. This is also the case. This area has long been known as the head process. The comparison of the primitive streak with the blastopore has proved a valuable idea. The importance of the idea is not diminished if we insist that the comparison does not hold at all points. The possibility of finding all three germ layers together at the margins of the blastopore (primitive mouth) is only fulfilled in the region of the primitive knot. Only the lateral margins of the primitive streak fuse with mesoderm, whilst the entoderm lying underneath has no connection. Therefore, one meets with objection to the homology of the primitive streak and the blastopore (primitive mouth) (K. Rabl). It is regarded only as a zone for the formation of mesoderm, which of course it is. The mesoderm has, in consequence, a threefold origin, gastral, peristomal at the knot, and peripherally from the primitive streak. If, however, the blastopore is represented only by the knot, then in meroblastic eggs would fail especially the lateral and ventral lips of the blastopore.

Para. 75. The peculiar form of the gastrula occupies the centre of our interest in these briefly described processes. It is also found extensively among the invertebrates and represents the most primitive differentiation of the animal body. All the antecedent processes of development are to be looked on as an introduction to this form. The essence of the gastrula is that, as a whole, it has a bilateral symmetrical form with the three typical axes (E. Haeckel). The mouth opening fails. The primitive mouth, considered from a comparative anatomical point of view, is a mouth or posterior opening (anus). The metazoa afterwards retain this opening as a single one or they form in front a new opening for the mouth. These may be distinguished as the protostoma and the deuterostoma (of Korschelt and Heider).

This difference is accompanied by others in the formation of the mesoderm and the cœlom. The deuterostoma forms gastral and peristomal mesoderm and an enterocœle. The protostoma possesses a very characteristic ectomesoderm and forms the cœlom either with or without the entoderm. Here therefore lie rooted formal agreements through which the vertebrates are joined with many classes of invertebrates.

The body wall of the gastrula arises from two layers, the ectoderm which functions as epidermis and sensory layer and affords relationship to the outside world, and the entoderm which as the gut epithelium subserves nutrition. The relationship to the outside world and the acceptance of nutrition establish the point of view from which we will judge this fundamental division of labour and differentiation for the whole animal organization.

Both sheets, germ layers, possess for the further development of the metazoa a great importance. From the ectoderm the epithelium, with skin, glands, hair, nails and the peripheral elements of the sense organs, are developed. Further the ganglion cells of the spinal cord and brain, spinal ganglia and sympathetic ganglia, neuroglia, nerve fibres and their sheaths, in some cases also smooth muscle (iris, sweat glands and cartilage cells) are developed. From the entoderm arises the epithelial lining of the alimentary canal and its associated structures (taste, organs of the mouth, bronchi, lungs, liver, pancreas, bladder), especially also red and white blood corpuscles. Also the entoderm gives origin to the mesoderm and so indirectly is the source of all the organs produced from this layer [para. 51 ff.].

The large or small amount of yolk in the egg modifies the development of the gastrula, so that it does not repeat the pure ancestral form but is modified cænogenetically. This modified gastrula is called the metagastrula (E. Haeckel). The pure archigastrula is almost exactly repeated in amphioxus. In the amphibia (fig. 38, *a*) in which the gastrula lies excentrically, and further includes the segmentation cavity as well, there arises an amphigastrula. In the meroblastic eggs on the contrary the gastrula lies as slit beneath the germinal area—it is a discogastrula (fig. 40). The layers actively increase and grow around the yolk mass instead of being invaginated.

We have now seen that the ways in which the non-mammals form their gastrulæ are very various. Through it all runs the idea of gastrulation. If we follow gastrulation as exhibited in the process in invertebrates and amphioxus there are presented for our judgment these questions:—

(1) If gastrulation is only invagination, then the formation of the cænogenetic entoderm and the formation of the deutenteron drops

out of the definition of gastrulation. On the other hand the formation of the chorda and the mesoderm in the sauropsida adds features which were not originally present in the conception of gastrulation. Gastrulation in the holoblastic and meroblastic sauropsida would then be two different things.

(2) If gastrulation is only equivalent to the establishment of a two-layered germinal area then invagination would no longer play a distinct rôle in the conception and would be joined in the ontogeny of higher forms with processes (chorda and mesoderm formation) which it does not possess in the development of more primitive animals where these processes first arise after the gastrula is formed.

(3) If one joins these two together then the process of gastrulation must be divided into two phases. The first forms the two-layered germinal area and provides the material for the head (brain, fore-gut); the second on the contrary forms the trunk (spinal cord, chorda, somites: Hubrecht, Keibel). The boundary between the two is situated at the otic vesicle. This modification would bring us to this result that holoblastic eggs form the head (fore-gut) through true gastrulation (cephalogenesis) and the trunk (notogenesis) by a process independent of gastrulation. The meroblastic eggs would on the contrary form the head without invagination, the trunk by gastrulation. The gastrulation process would then not be homologous developmentally in the two cases, but in each would furnish the part of the body which is the most dynamic.

Through these transitions the conception of Haeckel, in itself so enticing, is judged to be in danger, even to become inadmissible (Strahl, Veit), and to cease to form the basis of our morphological understanding of the embryonic structure of the vertebrate body. According to the original conception of Haeckel, not gastrulation but the gastrula should be compared, then the gastrula is actually an embryo in possession of the primitive gut. Accordingly we have to describe and recognize the formation of the primitive gut quite simply as gastrulation. The organism follows many different paths for the attainment of this purpose. This is due to the yolk content of the egg, to the peculiar form of growth of the primordia, and to the different modes of cell division. These are often widely different in different eggs, but the reasons are quite unknown (p. 287 and para. 82). The two particular phases in the primitive development of the embryo are both growth phases. Head and trunk formation are grouped around two centres of growth. The brain (the transverse brain growth) arises always, and along with it the later anterior pole of the body, in the region of the animal pole from the ectoderm. Up to this point the primitive gut, whether archenteron or deuteron, increases. This anterior portion of the primitive gut forms later the head fore-gut. The trunk surface (spinal cord, chorda, primitive vertebra and the rest of the gut) are formed caudally, and the more posteriorly the more it is formed from indifferent material (that is the first differentiation appears immediately in front). There is not always found in this part of the body a displacement of cell material towards the middle line and a fusion of growth (concrescence). On the contrary the tail arises from material displaced from both sides towards the middle line and from there it becomes elongated.

(b) Formation of the Fœtal Membranes.

Para. 76. The previous considerations are of service in understanding the principles of development in mammals and in man. In many mammals and in man the earliest development has this peculiarity, that it is associated most intimately with the development of the fœtal membranes. The development of these membranes begins in the earliest stages of development. In fact one can say they begin with the division of the ovum, whilst in non-mammals they are much more independent processes. This mode of development places many difficulties in the way of understanding. We will first describe the development of these membranes.

The starting point of the formation of all these membranes is the yolk sac, with whose morphology the beginner must make himself fully acquainted. Only then is an understanding of the complicated membranes possible (fig. 45).

The yolk sac in its ancestral form is the thickened, shapeless ventral surface of the embryo. It arises from the remnant of the macromeres taken into its interior. Since the egg yolk does not undergo division the yolk mass hangs ventrally in the membranes which envelop it as an almost complete sac.

Originally in the meroblastic egg, the gut is formed on the ventral side through the undivided yolk. After the germinal area is enclosed with ectoderm and the cœlom has developed between ectoderm and entoderm bounded by the two layers of mesoderm the embryo becomes elevated above the yolk. The embryo, originally formed altogether from the dorsal surface, attains lateral surfaces and also a ventral surface, the largest part. The gut in front and behind becomes a tube, but in the intermediate area remains, by means of a canal, in relationship with the yolk sac. At the same time the body wall and the space arising between the body and gut wall, the cœlom, are continued into the yolk sac.

So we find the yolk sac consists of an outer wall, somatopleure, and an inner gut wall, splanchnopleure, and between these a cavity continuous with the cœlom (the extra-embryonic cœlom). Both the outer and inner walls arise from the same layers as the walls of the body with which they are continuous, that is the outer from the ectoderm and its supporting elements; the inner from the entoderm and its supporting elements. The connection between the yolk sac and body is often broad and short, often more round like a handle (yolk sac stalk). The junction of the yolk sac with the body is the umbilicus, in which one, of course, distinguishes a skin and a gut umbilicus. That the yolk sac of this form is nothing other than an evagination of the body wall is shown by the fact that it finally enters the wall of the body completely.

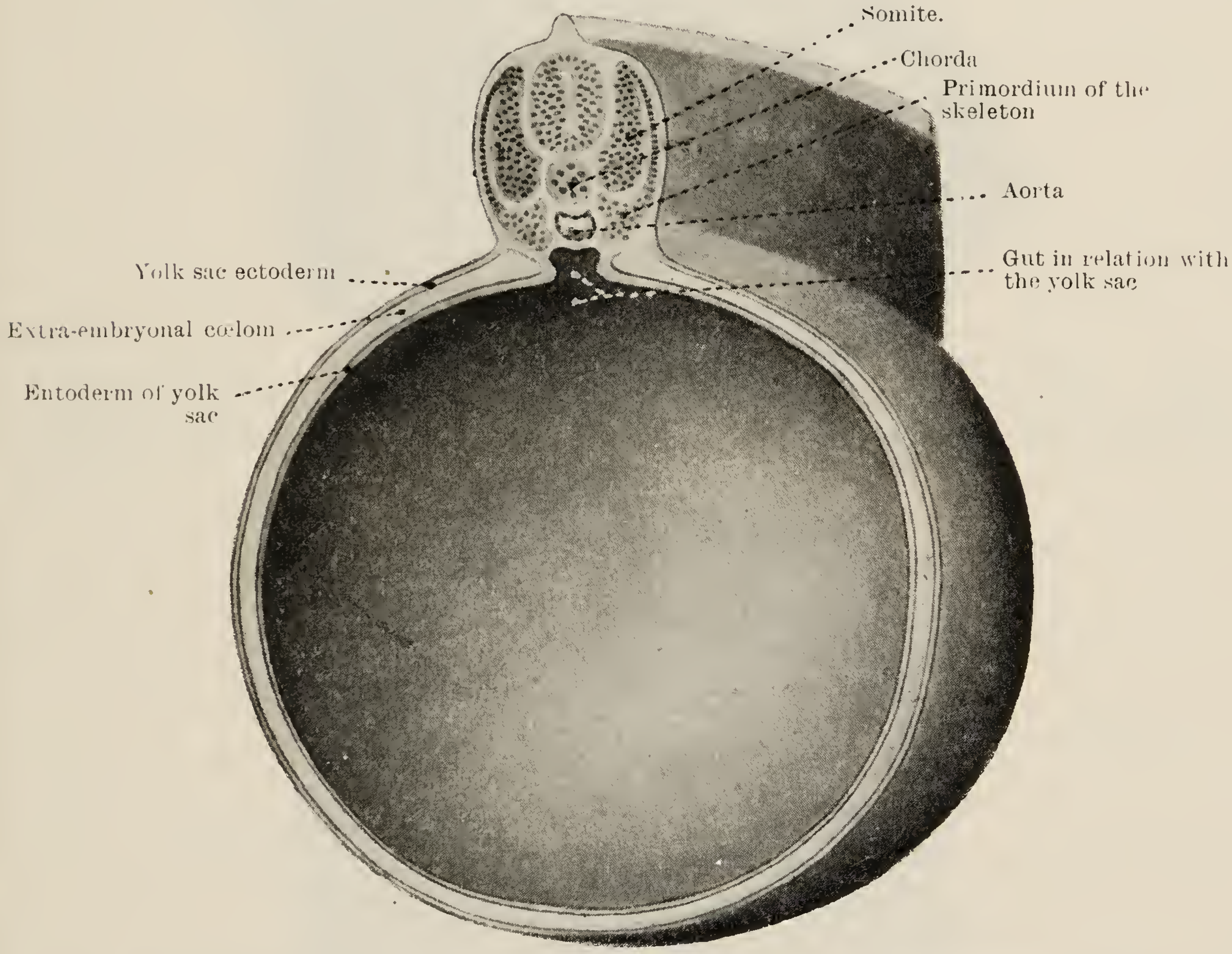

FIG. 43.—Schematic representation of the yolk sac of a trout embryo. The transverse section of the embryo from my own specimens and a figure in the textbook of O. Hertwig.

Beside the growing body it becomes imperceptible and finally forms a part of the ventral surface of the embryo. The inner wall of the yolk sac becomes the gut wall, the outer wall becomes the abdominal wall, the extra-embryonic cœlom becomes included in the intra-embryonic cœlom, and finally the contents of the yolk sac become alimentary contents and are absorbed. In this way the final stages in the meroblastic egg are the same as in the holoblastic egg.

If the yolk sac from a morphological point of view is a cæno-genetic structure (p. 322) yet from the physiological point of view it is a most important one. It functions for the embryo the same as the yolk-laden entodermal cells do for the holoblastic egg. Since the fish breathes by means of gills it uses its yolk sac only for nutritional purposes. For the transport of the nutriment the vessels are available which develop between the entoderm and its connective tissue layer. Before all it is to be expected that a vein on each side should run on the ventral surface of the gut (subintestinal vein). This vein, the precursor of the portal vein, laden with nutritive material, runs to the heart, previously passing the liver. This vein possesses also an extra-embryonic portion.

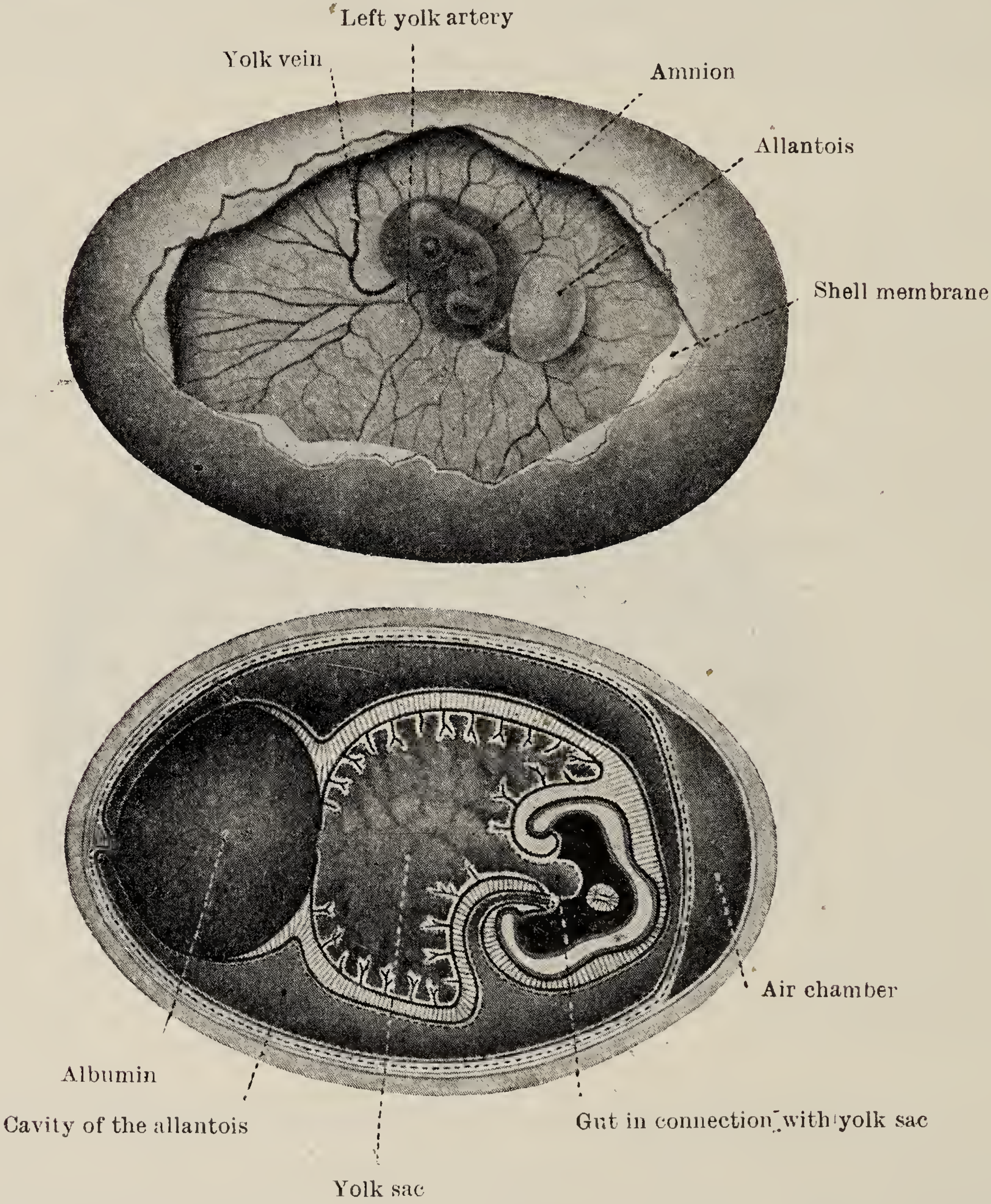

Fig. 44.—Egg membranes and accessory organs of the chick. Above the complete picture drawn from nature by Herr W. Freytag, University artist. Below, longitudinal section of a somewhat older egg adapted from a figure of Corning.

Since the embryonic body in the reptiles and birds is first formed indirectly by constriction from an undivided portion, it is clear that they must also develop a yolk sac. The anatomical relationships of its connections are the same. So long as the embryo is small the vascularized surface of the yolk sac is visible to the observer (the beautiful figure of the area vasculosa of the chick, fig. 44, upper). The

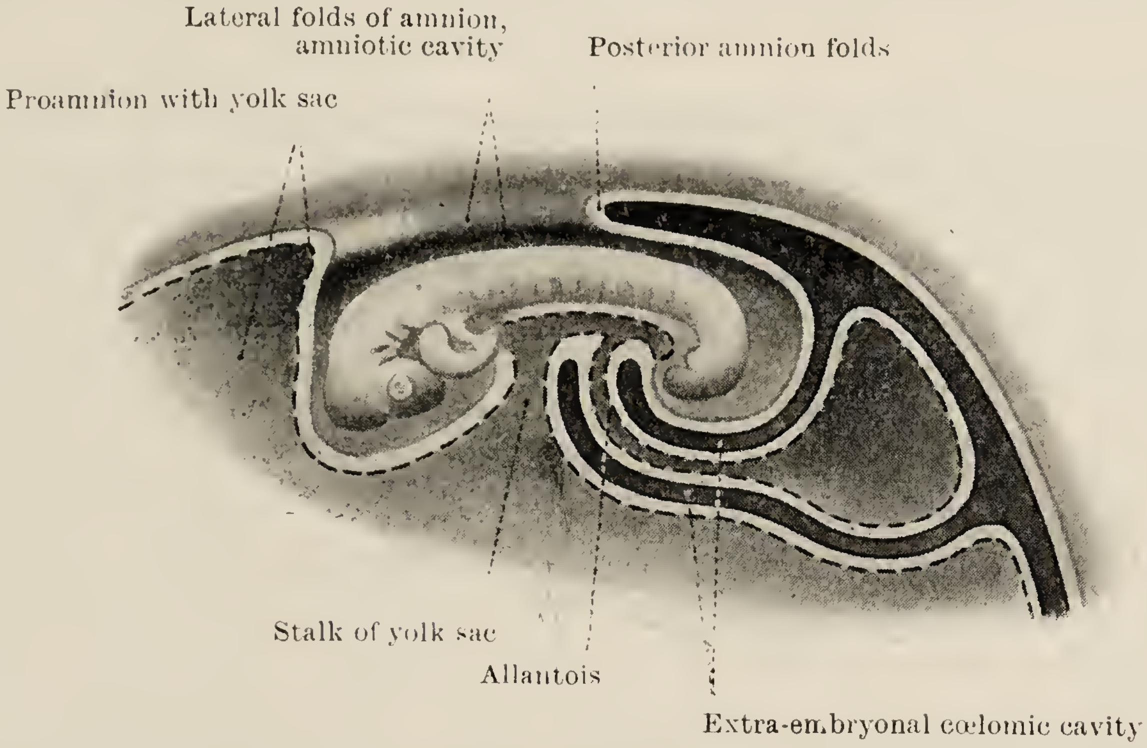

FIG. 45.—Cf. also fig. 49. Amnion formation in the rabbit, schematic. Behind extra-embryonic cœlom containing the allantois. Ectoderm grey; entoderm broken black line; mesoderm continuous line. Yolk sac light grey, extra-embryonic cœlom dark grey.

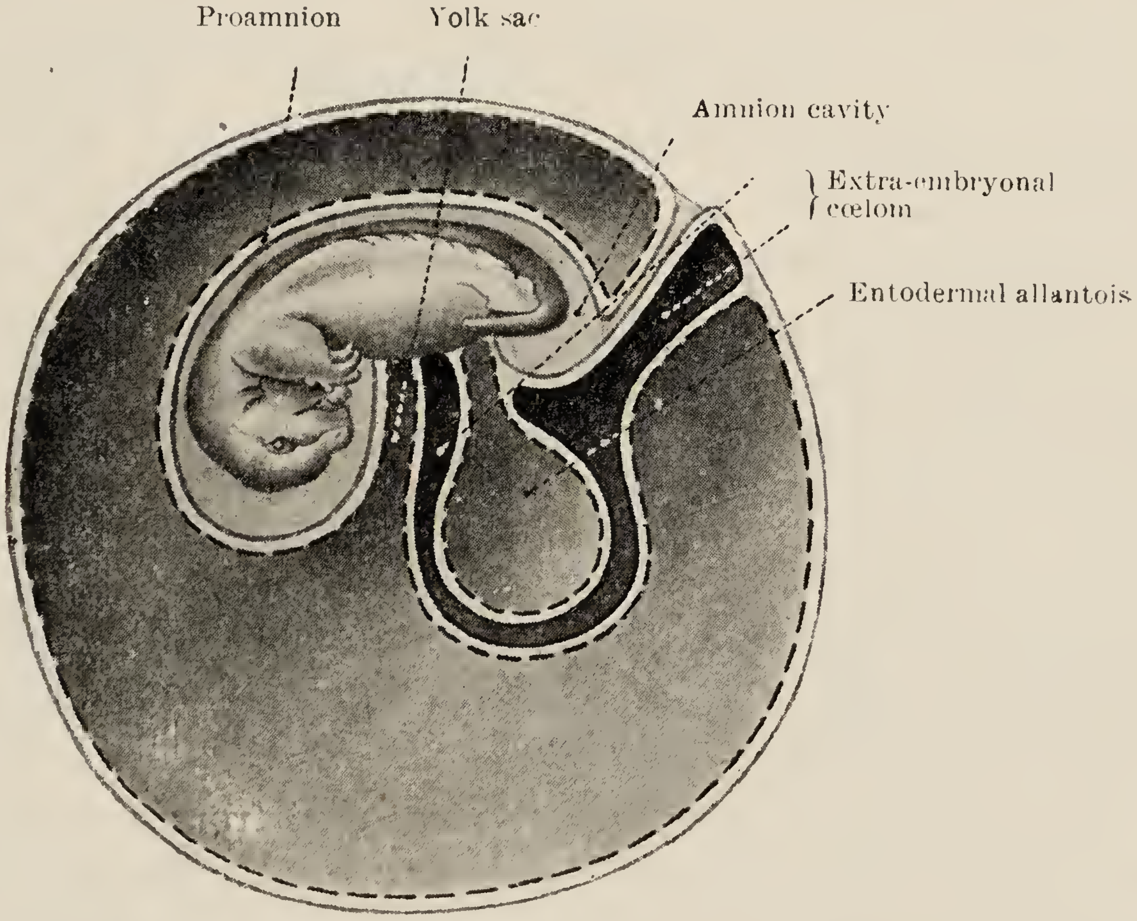

FIG. 46.—Egg membranes of the opossum (Didelphys) after Selenka. Indication lines as in fig. 45. Explanation in the text.

vessels separated from the shell only by albumen can continue in the service of respiration ; when, however, the embryo grows and the yolk becomes used up the relations alter. The yolk sac becomes removed from the neighbourhood of oxygen and functions only in nutrition.

As a nutritive organ it undergoes great differentiation. The cells are folded like the gut epithelium and arranged in lamellæ which protrude into the yolk. The cells of the yolk entoderm are laden with nutritive material and intimately related to the vessels. A remnant of the yolk sac persists finally in the animal after birth where it can be observed for a long time. Finally it becomes completely absorbed.

Para. 77. The outer wall of the yolk sac behaves differently in the birds and reptiles. The slit-like extra-embryonic cœlom in fishes presses round the embryonic body and forms the cavity of the amniotic folds, two lateral and one posterior (fig. 45). Where the margins of the folds join arise two membranes, amnion and serous coat (the chorion). The amnion lies over the embryo. This swims in the amniotic fluid. At the umbilicus the amnion fuses with body wall as previously does the outer wall of the yolk sac to which it corresponds. The exocœlom separates the amnion and the serous layer (fig. 45). Opposite the lower pole of the egg the chorion which surrounds the whole egg must behave as does the outer wall of the yolk sac, that is, it reaches always as far as the exocœlom is pressed backwards.

The anterior portion of the amnion behaves differently. Here the exocœlom does not reach in the beginning and so the ectoderm and the entoderm lie in contact. Here in the so-called pro-amnion the head pushes into the yolk sac and indents the wall of the yolk sac (head fold, figs. 45 and 46). It is, however, in the sauropsida that the exocœlom advances so far always that the pro-amnion is transformed into a true amniotic fold and divides into amnion and serous membrane. This invisible pro-amnion of birds and reptiles is of much morphological significance in mammals [para. 79].

The embryo is now perfectly excluded from the outside world in two ways. The yolk sac suffices for its nutritive, but not for its respiratory, needs. For this purpose in all sauropsida the allantois is developed. This is a sac developing from the hind gut, therefore from entodermal epithelium. It lies in the cœlom (figs. 44, 45, 46), and afterwards along with the yolk sac receives a covering of mesoderm from the splanchnopleure of the yolk sac. The allantois grows out in hernia fashion from the yet unclosed body wall and proceeds on the right of the embryo into the exocœlom. It then enlarges, firstly outwards beside the caudal pole of the embryo, and finally presses aside the whole extra-embryonic cœlom where it gets between the yolk sac and the amnion, gets beyond the chorion and lies on the shell of the egg (fig. 44, lower).

The form of the bird's egg is then finally that in fig. 44, below. The serous membrane lies in contact with the porous shell of the egg. Immediately internal to this lies the allantois, whose outer surface fuses with the serous membrane. Its inner wall fuses with the amnion and the yolk sac. The white of the egg is thus pressed to one pole and even surrounded by the allantois. In the wall of the allantois develops a second and new circulation, the allantoic or umbilical circulation (two arteries and one umbilical vein). This circulation extends around the internal surface of the shell and functions as the respiratory organ of the amniotic embryo. Especially does this circulation attain the function of absorption as it does in mammals and also in the sauropsida, since it absorbs the egg white. After birth the allantois and the egg membranes disappear in so far as they are extra-embryonic (through shrinkage and decomposition). The intra-embryonic part of the allantois becomes the bladder and the urachus.

(2) Primitive Development of the Mammal.

Para. 78. The primitive development of the mammal is remarkable in that it develops from a holoblastic egg. It reaches an end stage with which the condition of holoblastic eggs of more primitive forms is not to be compared. The first segmentation naturally is not often observed. It shows the astonishing rule that the further divisions of the first two cells are not contemporaneous. Cell stages of three, five and seven are found interpolated between two, four and eight cell stages (Sobotta).

As examples of further development a series of the field mouse is available (van Beneden). Quite early some of the dividing cells are distinguishable by their clear appearance from others which are darker (fig. 47,a). In between the growing cells spaces arise (fig. 47,b) and the clear material is pressed to one point (fig. 47,c). The spaces fuse into a single cavity which has now a thickened plate over it (figs. 47,c and 47,d) and on the opposite side is covered by a cell sheet that is at first single and then double. This cell sheet also passes over the thickened mass. From the thickened cell mass there is formed a broad layer of cells, at first loose, later more compact (fig. 48), the internal lining of the hollow space.

It is clear that the labels, blastula, ectoderm and entoderm for fig. 47,c would not be sensible. If it were a blastula then the plate of thickened cells would represent nothing comparable to the sea urchin or amphioxus blastula. Also the internal protrusion of cells would not be understandable without further explanation. If the surrounding cells were ectoderm then this would comprise two layers which would not correspond to the form of the blastula.

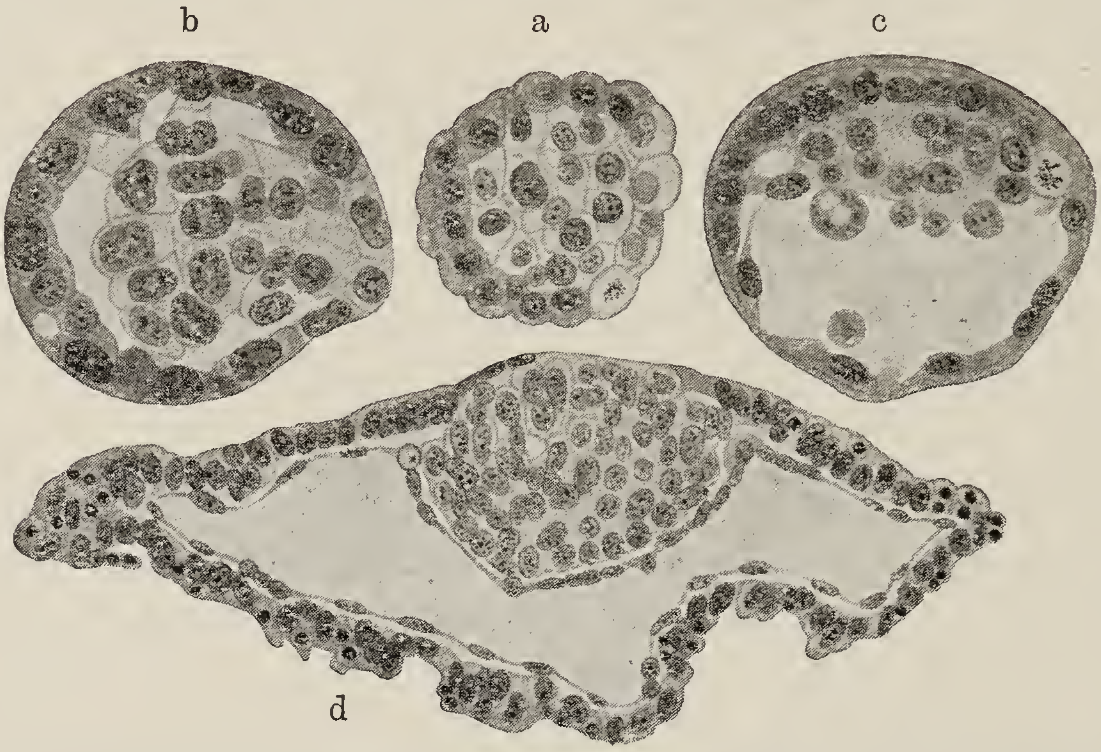

Fig. 47.—Segmentation, formation of the blastocyst and of the two layered embryo of the bat (Vespertilio) after van Beneden. Explanation in the text.

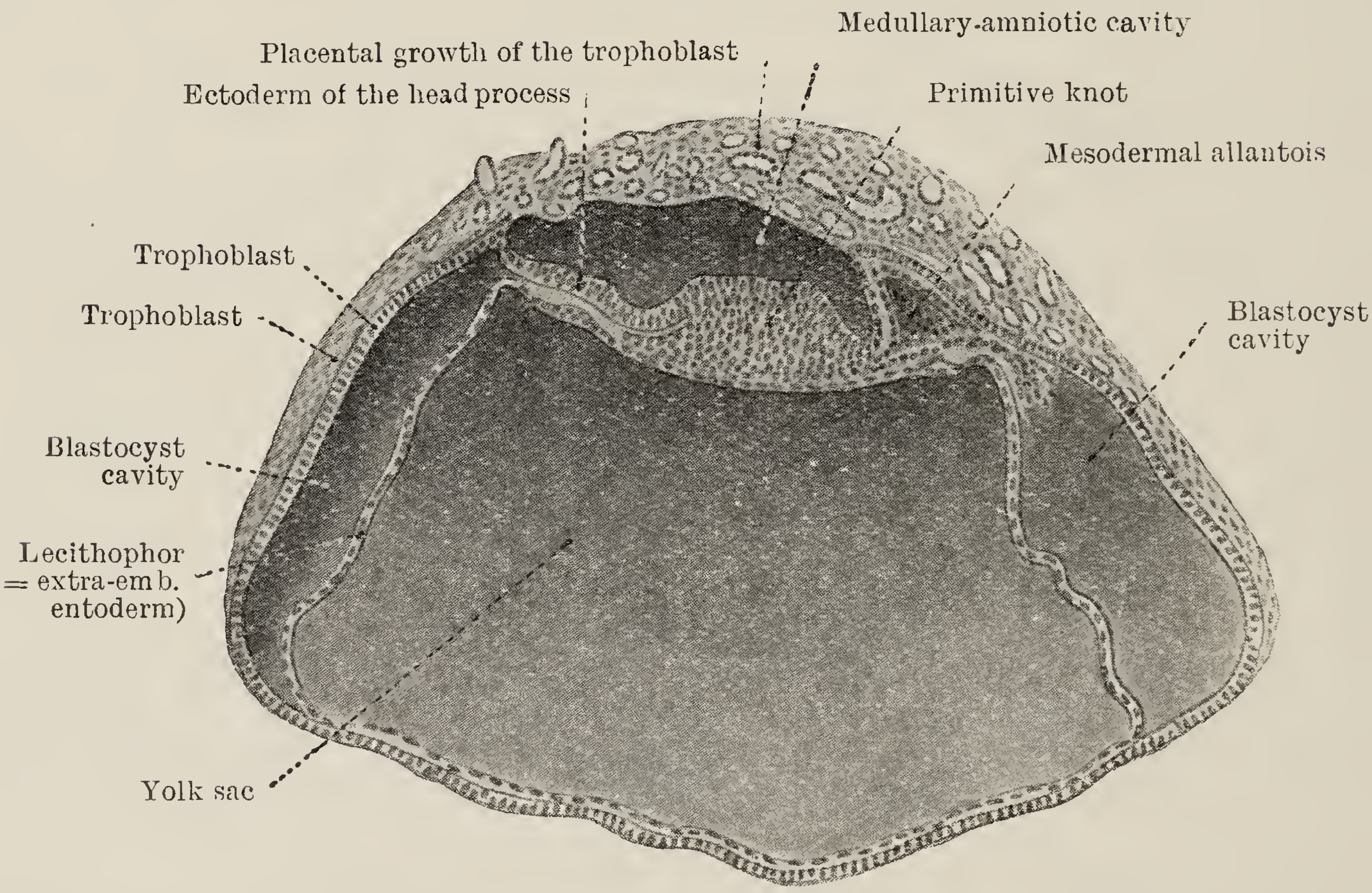

Fig. 48.—Embryo of Vespertilio at the stage of the formation of the primitive streak and head process. Longitudinal section through the bilaterally symmetrical primordium, anterior end on the left. Medullary amniotic cavity. Diplotrophoblast, placental site, after van Beneden. Explanation in the text.

However, figs. 47,c, 47,d and 48 are easily understood so soon as one remembers that it is a cavity filled with yolk. Then the thickened cell mass corresponds to the germinal disc and the cell sheets surrounding the hollow cavity (which are here two-layered to the extra-embryonal ectoderm and entoderm, fig. 48). Indeed the development of the mammalian ovum is only properly understandable if one makes it clear that mammalian development only began when the mammal produced the yolk-rich egg which had not to be passed to the exterior, but went through an internal development in somewhat the same manner as the salamander eggs now do in developing into larvæ within the uterus. This intra-uterine method of development has not led to the suppression of the yolk-laden egg, but has brought about a reduction of the yolk by a diminution in size of the egg.

For a proper appreciation of the important stages of the early development of the mammal the following points should be borne in mind :—

(1) The stages of figs. 47,b, c, d, and 48, ought not to be described as blastula. As an intercellular space (virtually filled with yolk) it deserves a special name, and following Rabl we will call it the blastocele.

(2) The thickened cell mass is comparable to the germinal disc. The material of the embryo comes only from this. It is called the embryonal shield or knot (not to be confused with the primitive knot of the primitive streak).

(3) The cell sheet which first encloses the blastocyst as a single layer is extra-embryonic ectoderm and known as trophoblast. Soon this trophoblast forms two layers called the diplotrophoblast; the inner one is the cytotrophoblast, the outer the plasmodial trophoblast; the third inner layer (the extra-embryonic entoderm of the hen's egg enclosing the yolk sac) is the so-called lecithophor.

The use of these names is desirable for the equivalent layers in the chick originate later through an off-growth from the germinal area, but in mammals they are derived continuously from segmenting material.

The whole three-layered form [fig. 47] (it is only two-layered since the trophoblast is yet single) can become extraordinarily large and is capable of being examined macroscopically. When its development was not understood this shaggy-like vesicle was taken for the Graafian follicle prolonged into the uterus.

The blastocyst may vary very much in form. Consider figs. 41 and 49,c and look first at the upper part of the figures. In both cases the germinal area is situated dorsally and below the cavity which in the case of the mouse is drawn upwards into two angles. The whole

(49,*c*) represents the stage of development of the gastrula of mammals whose entoderm arises entirely as cænogenetic entoderm, whose cavity is also a real deutenteron. True invagination as it occurs in the reptiles and birds will at all events be observed as the exception. In fig. 49,*c* the canal arises through true invagination, a tiny archenteron that opens into the much larger deutenteron (fig. 49,*c*) on the right. The canal starts from a primitive groove; on the right of this lies the primitive streak. In fig. 48 the rudiment of the embryo is cut longitudinally, head part lies on the left. The thickening is the primitive knot.

If we ignore the great differences of the fœtal membranes, the primitive development of the axial organs (the neurula) is without essential difference from that of the reptile and bird. Whilst in the reptiles and birds the development of the embryo and the membranes is especially easy to demonstrate, it is not always possible to do so in the mammals. The development of the rabbit (figs. 45, 49,*a*) and the carnivora confirms this, for the development of the amnion and the allantois is the same as in the chick. This shows that a morphological continuity exists between the sauropsids and the mammals; they form a group of amniotes.

Para. 79. The yolk sac in mammals is called the umbilical vesicle. There are many degrees in its formation. It is largest in the marsupials where it can surround the whole embryo, including the amnion and the allantois (fig. 46). In these it is the yolk sac that lines the whole of the uterine cavity. In the carnivora, ungulates and rodents it reaches a middle size. In man and the primates it is extremely small (p. 290). It appears as if the yolk sac as the organ of nutrition and respiration stood in respect to size in inverse relationship with the allantois. The size of the yolk sac must, however, stand in inverse relationship to the size of the extra-embryonic cœlom too. For if the yolk sac be large as in marsupials, the extra-embryonic cœlom can be small as in the chick (figs. 46, 49,*a*). In other mammals (fig. 49,*b*) the cœlom extends further forwards than in fig. 49,*a*, but not so far downwards as in the chick. Where the umbilical vesicle is small the exocœlom surrounds it on all sides, and it hangs free in the exocœlom (Primates, para. 82 and fig. 56). For the appreciation of all these facts numerous factors must be considered, for even among the Primates there arises great variety of form: predominance of yolk sac or placental nutrition earlier or later, perfect or imperfect imbedding of the ovum in the wall of the uterus.

The function of the umbilical vesicle is also various. It is nutritionally large, of great extent and of the same value as in non-mammals, in the egg-laying monotremes and everywhere in mammals where the placental nutrition is of small moment. Also where the placental nutrition is dominant the yolk sac has often a special nutritive function in that its cells take up extravasated blood which is poured into it (embryotrophe), and carry this to the embryo (Sobotta). Where, as in the Primates, it has not to do this, it is a rudimentary organ only, a witness of the formal plan in the construction of the embryo; also the yolk vessels add witness that in these cases the yolk sac has only an insignificant part to play (in contradistinction to the sauropsids where there is a yolk artery with a yolk vein on each side).

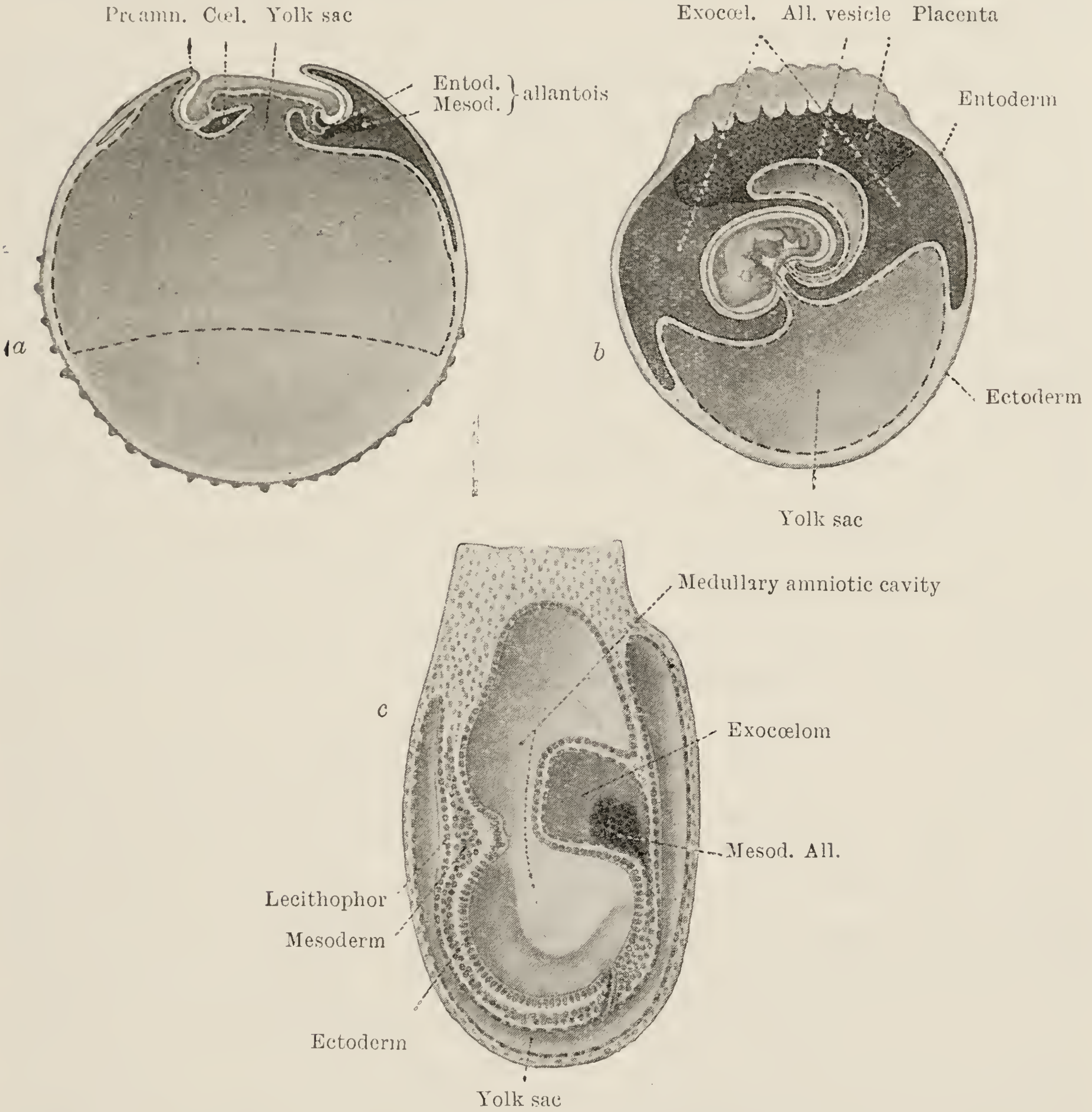

FIG. 49.—Types of formation of the yolk sac, the allantois and the amnion in mammals. On the left above, the rabbit, according to van Beneden. Differs from fig. 45 (schematic) only in that towards the front, in the region of the primordium of the heart an extra-embryonic cœlom widens out. On the right above, Vespertilio, according to van Beneden. Below, the mouse, according to Sobotta. The indications as in fig. 46. Further details in the text.

Besides the nutritive there is also a respiratory function of the yolk sac, at any rate originally. In mammals, though in changed form and manner, it is not absent, though under intra-uterine conditions it is not in relation with the atmosphere. Its wall and its vessels can take over the function of the allantois wherever the wall of the yolk sac immediately lines the ectoderm and so lies on the uterine wall (fig. 46).

The allantois is in most mammals a sac as in the sauropsids, which stretches into the cœlom (figs. 45, 46, 49,*b*). Its wall arises from entoderm and splanchnopleure. Between both layers is developed the mesenchyme and the umbilical vessels. It cannot, as in the sauropsids, extend along the shell, but it does come into relationship with the maternal vessels of the uterine wall. It forms villous-like elevations wherever it comes into contact with the placenta. It is remarkable that in the mammalian orders, where there is a precocious development of placental nutrition, the more perfect this is the more the proportions of entodermal sac and mesenchymatous wall become reversed.

The entodermal sac (entodermal allantois) is very small in these cases in proportion to the mesodermal wall (mesenchymatous allantois). In the Primates it is reduced to a very tiny canal within the massive mesenchymatous wall (fig. 56), which is functionally the most important part.

Para. 80. The amnion formation of many animals, for example, the rabbit, can easily, as has already been remarked, be referred back to that of the bird (figs. 45, 49,*a*) ; the agreement consists in the fact that the process which gives rise to the true amnion folds, namely, the pressing forwards of the exocœlom, ceases first in the head region (proamnion, the prokalymma). This last condition is achieved later in the rabbit also and in some marsupials reaches so high a degree (fig. 46) that the amnion is formed of ectoderm and entoderm only, and the embryo protrudes into the yolk sac. In most orders, however, through the forward pressing of the exocœlom a true amnion arises as in birds and reptiles. Because of its fundamental importance for the formation of the fœtal membranes in man, and because of the light it sheds on the formation of the amnion, we must review the mode of amnion formation. It is that process to which we have referred at the beginning of our presentation of the fœtal membranes. In some mammalian orders (rodents, insectivores, cheiroptera, primates, man) the amniotic cavity arises not from the fusion of folds but by the formation of a cavity in the cell mass of the embryonal knot.

This cavity at the beginning is an intercellular split within a layered epithelium. It arises within the knot (fig. 47,d) and raises later (figs. 48, 49,*c*) the roof sheet from the rest of the knot. The floor of the slit is formed by the embryo, on which the medullary folds are later elevated. (The epithelial cells oppose their free surfaces to the cavity). The roof is formed by trophoblast.

This cavity has been called the medullary amnion cavity (primary amnion cavity, false amnion cavity), because the cavity includes more than the true amnion cavity. Only when the medullary folds have fused does it include the true amnion cavity. However, we ought to designate this a true amnion if it arises from the two layers which comprise the outer wall of the yolk sac, that is if the ectoderm has received an outer covering of mesoderm. This appears essentially in the same manner in birds; the cœlom presses forward extra-embryonically (fig. 49,*a* on the right, fig. 48 on the right) and splits the mesoderm. So soon as the extra-embryonic cœlom surrounds the whole amnion the serous membrane is formed. Its outer layer is the trophoblast; it forms epithelial villi (primary villi) (fig. 56,*a*), the mesenchyme invades these (secondary villi) ; hence the name chorion, the villous membrane. In the ectodermal part of the chorion, that is the trophoblast, two layers are formed, the roof sheet which extends as a syncytium or plasmodium (plasmodial trophoblast) and a deeper sheet which consists of defined cells (cytotrophoblast). The trophoblast in its entirety in the placental mammal possesses tissue-dissolving and tissue-destroying properties. Accordingly, it makes room for the growing blastocyst, and creates a tissue flow whose elements are taken up by the cells of the trophoblast directly, or through the yolk sac in which it first accumulates (e.g., mouse, Sobotta). It is then carried to the embryonal vessels and serves for the nutrition of the embryo, embryotrophe.

Para. 81. We now adhere to the view that all organic structure must show a continuity and unity of development, and at the same time at all stages exhibit a functional worth ; then the question of the formal significance of the fœtal membranes steps into the foreground of interest.

How and in what way does it come about that the embryo of the amniotes floats in an amniotic cavity filled with fluid, and that a secondary nutritional system (umbilical circulation) in the wall of a sac (allantois) finds its way into the serous membrane (chorion) in order to form in the wall of the uterus the most perfect nutritional apparatus it is possible to imagine ? The answers to these questions, as to all great morphological questions, are and must be purely hypothetical. They have never been made overt in development, and the causal connections long since lost can no longer be reconstructed. They can only be divined by comparison and combination. Such a combination can be accomplished in many different ways naturally, but the value of this will depend on whether it includes all the known facts, and whether all the phenomena can be related in a causal chain. A basal principle of all hypotheses on the phylogeny of the membranes must insist, under all circumstances, on the unity of their origin. It is scientifically unacceptable that the membranes, which, in their final condition, agree so perfectly, could arise independently. Further, we must take for granted that only an amnion closed and filled with fluid is of any value to the embryo. Then it is not the development of the amniotic folds that is of heritable value, but it is the closed amnion sac that is of value, so that the egg can proceed with its development in the air independent of the atmospheric pressure, just as the eggs of fishes and amphibia within a tertiary membrane develop in water (jelly, shell, &c.). With correctness the point in time when the change in surrounding medium occurred, when the animal laid its eggs, not in the water but on land, has been accepted as the time when the formation of the amnion must have arisen. Since the egg pursued its development in the water it is difficult to imagine how the development survived when the atmospheric pressure weighed on the germinal area if there had not been some compensation. Here, however, lies the difficulty in forming hypotheses, for one can now proceed in two ways, according as one regards the membranes of the sauropsids or those of the mammals as primary. If one accepts the former then all the stages which begin with the closed amnion are absent; if one accepts the latter then those mammalian orders which we are accustomed to regard as the highest forms would be the most primitive in their development. Since of the numerous ways out of the dilemma no conclusion is possible, we can proceed at once to an individual account of the phylogeny of the membranes of the amniotes.

On the first way the attempt has frequently been made to arrive at a coherent view of the formation of the amnion. The view that the folds have arisen in order to form the membranes for the water bath of the embryo, which is referable to the standpoint of the Lamarckian, only brings the findings in the chick to its disputed position in the phylogeny. At the same time it throws no light on important morphological facts, above all that of the pro-amnion, i.e., the fact that the head of all sauropsid embryos in the beginning protrudes into the yolk sac. There are more valuable mechanical factors to bring forward. The formation of the allantois will bring about the elevation of the folds, though a different interpretation is possible, for it may be that the formation of the amnion precedes the formation of the allantois. A further possibility is that the embryo developing in the air sinks in the specifically lighter yolk and so is surrounded by folds. However, Semon has brought forward proof that the embryo is specifically lighter than the yolk. Semon has further suggested that the growth of the head end directed downwards more strongly in the amniotes than in the anamniotes bores the head into the yolk and so creates the anterior fold of the amnion. Granted all this, it still leaves the formation of the amnion as a whole unexplained. Nothing is gained by following these speculations any further. The difficulty is increased if we derive the relations of the amnion in the mammals from some primitive process which is totally unknown to us. If we accept that the formation is due to the intra-uterine position there still remains the question why the rabbit forms its membranes like the chick, and others again form a medullary amnion, and others again something intermediate between the two. The question arises here as to what starts the formation of the allantois. One might imagine that the respiratory function of the bladder is not more wonderful in itself than that of the gills and the fore-gut, since it uses the respiratory capacity of the gut epithelium. As the pharynx forms gills and the fore-gut forms lungs, so the hind-gut forms a cloacal lung, which attaches itself to the umbilical circulation as the bronchial wall attaches itself to the pulmonary circulation. Here, however, the objection may be raised that there is no gaseous exchange in the allantois as there is in the lung between the vascular system and the contents of the vesicle, but between the vascular system and the outside world. The entodermal allantois, as urinary bladder, is genetically beyond our understanding, if we see in this its principal purpose as in the chick and rabbit, in whose wall has developed the respiratory umbilical circulation. On the contrary, a mesodermal respiratory allantois, as in most mammals and in man, is physiologically understandable in so far as we can establish some probability of its mode of development, and the way in which the entodermal elements become reduced.

Such a starting point a new hypothesis (De Lange) which replaces an earlier one of Hubrecht's may be able to furnish. By it, it is possible to explain the whole membrane morphology. Though there are many lacunæ in it and it does not resolve all difficulties yet it is of more general value throughout. The central point of this hypothesis is the idea that the oldest amniotes possessed eggs which have been enclosed in triple-layered membranes, and like, for example, the egg of the salamander, have perfected their development in the uterus.

Such an egg (fig. 50,a) has the whole of its yolk sac functionally adapted for nutrition, and the circulation has become markedly developed at the ventral lip of the blastopore. This endows it with the possibility of metabolic and gaseous exchange with the wall of the uterus.

A further stage is assumed to follow, which (fig. 50,b) after atrophy of the triple membranes brought the yolk sac into immediate contact with the wall of the uterus. This new direction to nutrition brings about the reduction of yolk nutrition and so the yolk sac gets smaller and the extra-embryonic cœlom larger. The outer wall of the yolk sac considerably thickens, its mesenchyme develops the umbilical circulation which forms at the ventral lip of the blastopore the large umbilical vessels. Its covering layer and its ectoderm become trophoblast, which enters into intimate relation with the wall of the uterus. Above all, the atrophy of the triple envelopes brings the embryo into the closed membrane, in whose shelter it had developed in the anamniotes, and at the same time allows the embryo to lie in close association with the wall of the uterus. This hypothesis

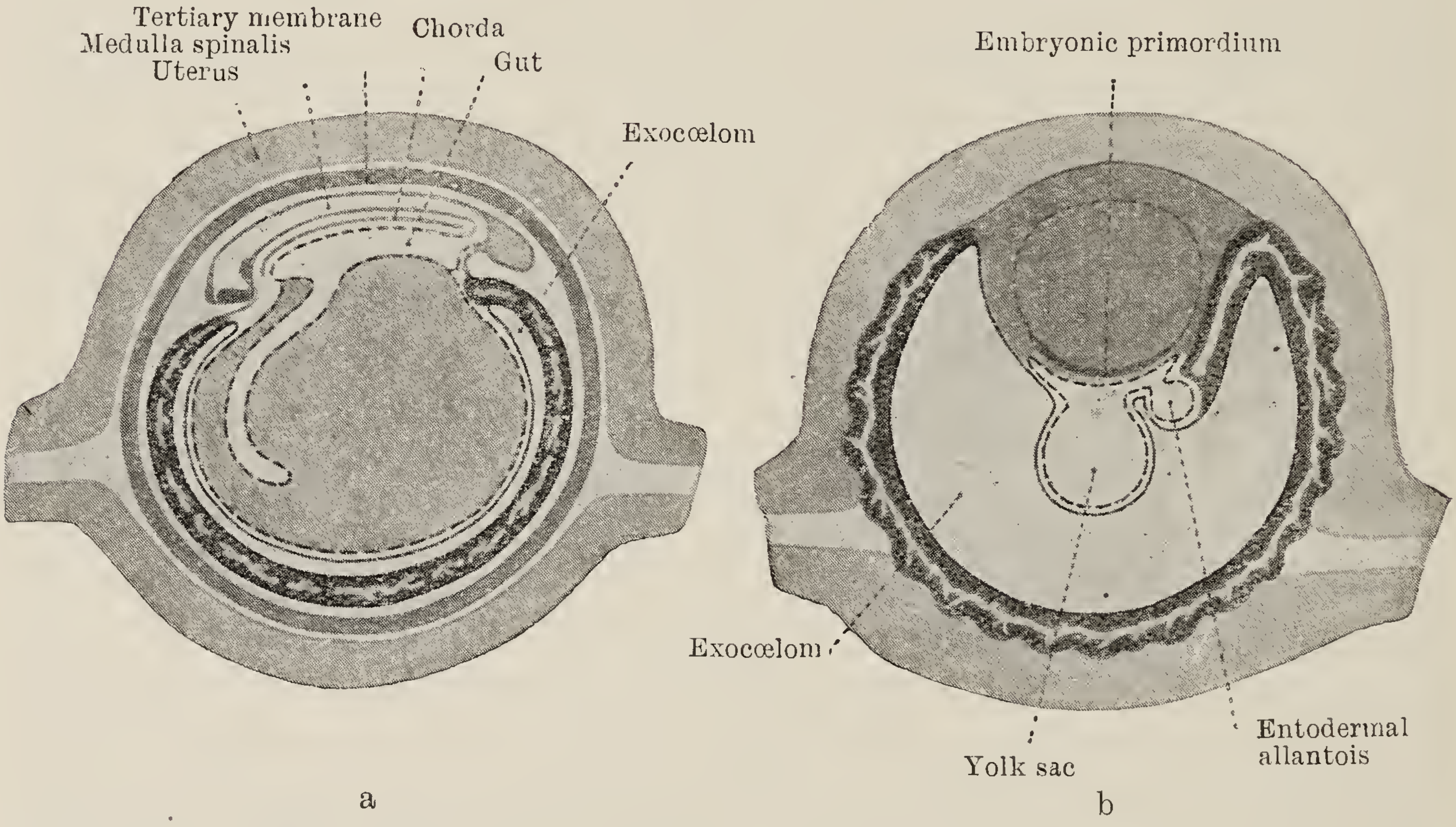

Fig. 50.—Schemata for the elucidation of the phylogeny of the amnion according to the theory of de Lange. Explanation in the text. On the left an amphibian embryo (according to de Lange) enclosed in the tertiary membrane (yolk membrane) and lying in the uterus. Extra-embryonic membranous fibre layer with respiratory blood-vessels. On the right a mammalian embryo (broad grey lines) with yolk sac and entodermal allantois in the extra-embryonic cœlom. Its gut fibrous layer lies immediately in contact with the uterine wall without any intermediate tertiary membrane. Marked growth of the ectoderm (broad grey area) carries the embryonic primordium into the extra-embryonic cœlom (entypy). The dotted circle indicates the later intercellular space which becomes the medullary-amniotic cavity. This representation is freely derived from the description of de Lange.

accepts that the marked increase of the ectoderm in the earliest establishment of the egg in the uterus forces the rudiment of the embryo as well as the small yolk sac into the now quite large cœlom. In this manner it has become concave (entypy of the embryo). The entodermal allantoic vesicle removes the metabolic products arising during development and suffices for this until the fœtus is separated from the uterus. Entodermal and mesodermal allantois should, on this hypothesis, be closely related in that the former, as a receptacle for the products of metabolism, is smaller in proportion as the metabolism is more fully dominated by the umbilical vessels. The larger, however, the entodermal sac the smaller the nutriment carried by the vessels and the more exclusively do they function in a respiratory manner.

The extension of the extra-embryonic cœlom appears as the third stage. In the solid ectodermal thickening arises, may be, an intercellular space. This would immediately provide the membranes in the form in which they are present in the primates and man. The position of the ventral lip of the blastopore and the marked increase of the umbilical vessels would be expressed in the so-called umbilical cord of the embryo (p. 291). In this the extension of the extra-embryonic cœlom would naturally find its limits. The medullary amniotic cavity is then, until the establishment of the umbilical cord, bounded by the outer layer of the yolk sac. The entodermal allantois is a narrow slit.

So far this hypothesis presents no insoluble difficulties. Less attractive are the further conclusions, though these admit of earnest discussion. It is now assumed that in those forms which had acquired the entypy as their inherited mode of development the attachment to the uterine wall is later. Here the entypy precedes the establishment in the uterus. The embryo becomes elongated, the roof of the proamnion becomes thin and the centre of gravity now lies in the extra-embryonic cœlom where the formation of the amniotic folds proceeds. The delay in the establishment of the trophoblastic nutritive process, which on the one hand the entypy makes possible, carries compensations on the other hand in the larger yolk sac and the entodermal allantois. The proamnion may then be the last indication of an entypy of the head part of the germinal area. So then the hypothesis proceeds to accept that the most intimate and the earliest relationship arising between the uterus and the germ is phylogenetically the oldest, and that the imperfect placentation, and especially the defect of such an arrangement, is phylogenetically the youngest. Oviparity, as in the monotremes and in the sauropsids, may then be the latest stage, so that the yolk sac of these animals is not immediately analogous to the yolk nutrition of the amphibia but may arise from the tertiary yolk-poor eggs of higher mammals as a tertiary yolk-rich structure.

This whole derivation contradicts the time relations of the facts. None of the known fossil animals of the Permian or Triassic period shows in surviving related forms an embryonal development which links it to primitive mammalian development. On the contrary we see that those forms which had the most primitive development arise quite late. The most primitive reptile (Hatteria) indeed exhibits an amnion development which forcibly recalls the medullary amnion development in its formation (cf. Schauinsland in Hertwig). Also it is to be recalled that the early development of many mammals, and especially of man, is in many points more primitive than that of birds [see para. 74]. So that the transition which this hypothesis forces upon us does not leave us quite in the air. We must remember that the phylogenetic link between the amphibia and the amniote organization does not lie in the salamander but probably very much deeper in the stegocephals known to us only as fossils. The genealogical relation [para. 40] of the forms is, in this case, very much more complicated than the simple stem lines suggest. It would be very short-sighted to estimate the phylogeny of the fœtal membranes on the basis of the developmental processess known to us, since naturally nothing is known of the development of the stegocephals and the fossil reptiles.

Whether the remains of small skeletons found with the ichthyosaurian skeleton are those of embryos lying within the uterus or of animals that have been eaten, is doubtful; probably the latter is the case (Abel).

(3) Early Development of Man.

Para. 82. A scientific understanding of the development of man is attained if one finds that its neurula repeats the neurula of the vertebrates, and if one can perceive clearly the way in which it has been formed. Traces of the early development of mammals are mixed with things purely human. Naturally we can only give a brief survey in the space at our disposal. We shall give a sketch of the typical and the specific human development and make it possible to overcome more easily the difficulties of the literature and the preparations.

Figures 51,a, b, c are hypothetical, since the segmentation has not been observed either in the primate egg or in man. The single exception is that of Selenka, who found a two-celled stage in cercopithecus. This shows a larger clear and a smaller darker cell. This agrees very closely with that of other known mammals (mouse, Sobotta), so we ought to accept a similar behaviour for the human egg. The human egg, whose transverse diameter is 0·2 mm., is one of the smallest. Figure 51,a is the four-celled stage. It shows the reversed position of three cells below and one above of all placentals (Sobotta). The cells are round and approximately of the same size.

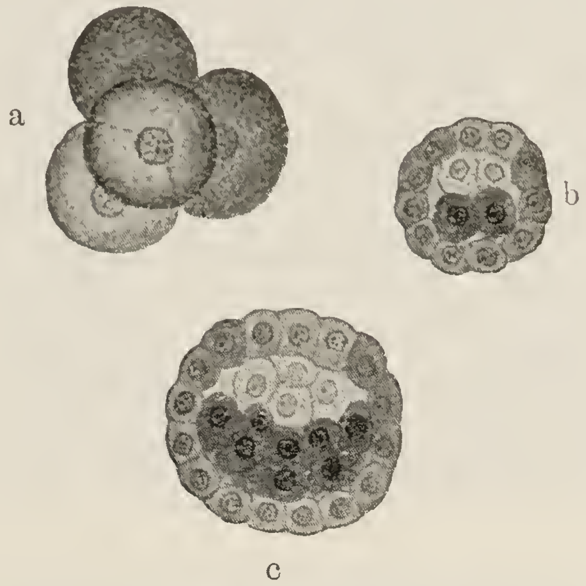

Fig. 51.—Hypothetical schematic segmentation (a) and morula stages (b, c) of man. The earliest beginning of the determination of the segmenting cells is indicated in b and c, by four different shades (cf. the explanation in fig. 45). Quite clear are prospective entodermal cells (yolk sac, lecithophores), light grey embryonic ectoderm, dark grey trophoblast, black extra-embryonic mesoderm. The stage, c, corresponds to that of fig. 47,b, if one turns around fig. 51,c with the upper pole towards the right; the whole cell mass (light grey, dark grey, black) produces the knot. The tones in 51,b and c are schematically printed different colours, the tones 51,a and fig. 47 are naturally occurring optical differences in the cells which should not be overlooked in considering the figures. Probably one of the dark cells of 51,a produces a part of the lecithophores, the three other cells all the remaining structures.

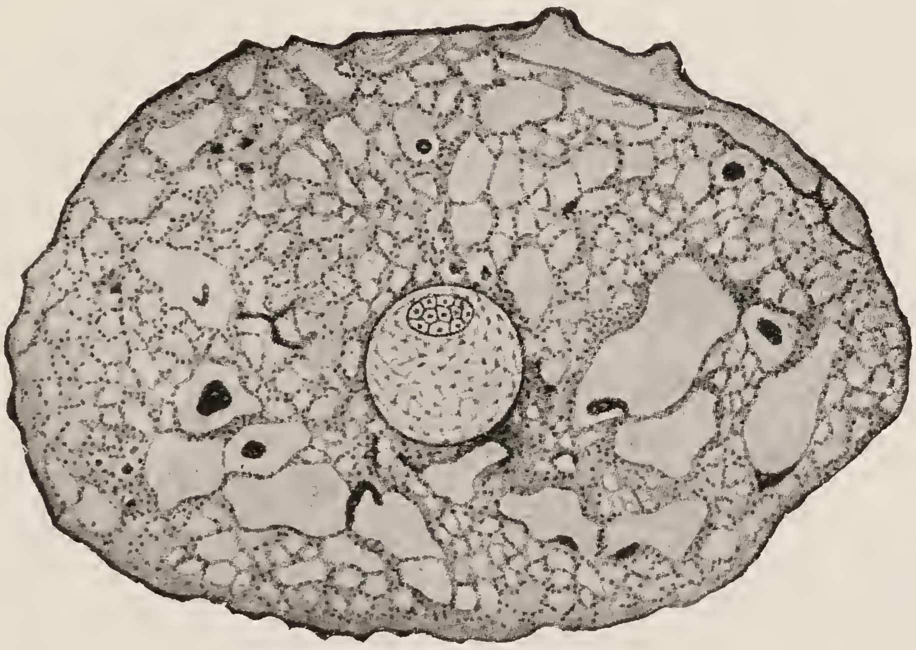

Fig. 52.—Scheme of the ovum by v. Mollendorff in the theory of Grosser (Ergeb. d. Anat., Bd. 25, fig. 4, 1924). Uterus and implantation site to be imagined in the above picture. The alveolar sheet around the egg is the trophoblast and destroyed uterine mucous membrane. Differentiation of the cells of the embryonal knot in the ectoderm and yolk sac (entodermal lecithophores) not recognized in the feeble enlargement. Around these cells the fine stretched tissue of the magma.

Two are darkly granulated and two are clear. Figures 51,b and c show the segmentation beginning, corresponding to the stage of the field mouse in fig. 47,b. The trophoblast and the embryonal knot

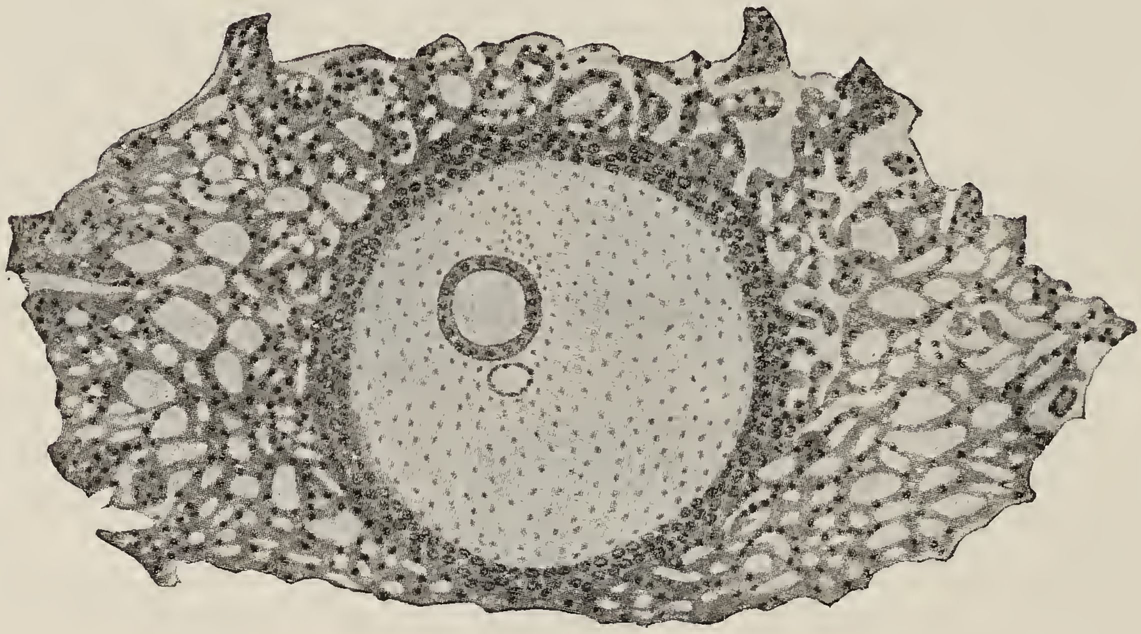

FIG. 53.—Scheme of the Bryce and Teacher ovum by Grosser (fig. 6). The ectodermal cells have given origin to the intercellular cleft of the medullary-amniotic cavity, the entodermal cells to the yolk sac. The extra-embryonic cœlom filled with magma (dotted); this and the similar picture in fig. 52 to be referred to the cells toned black in fig. 51,c. Likewise the medullary-amniotic cavity is to be referred to the light grey, the yolk sac to the white, the trophoblast to the dark grey cells of this figure.

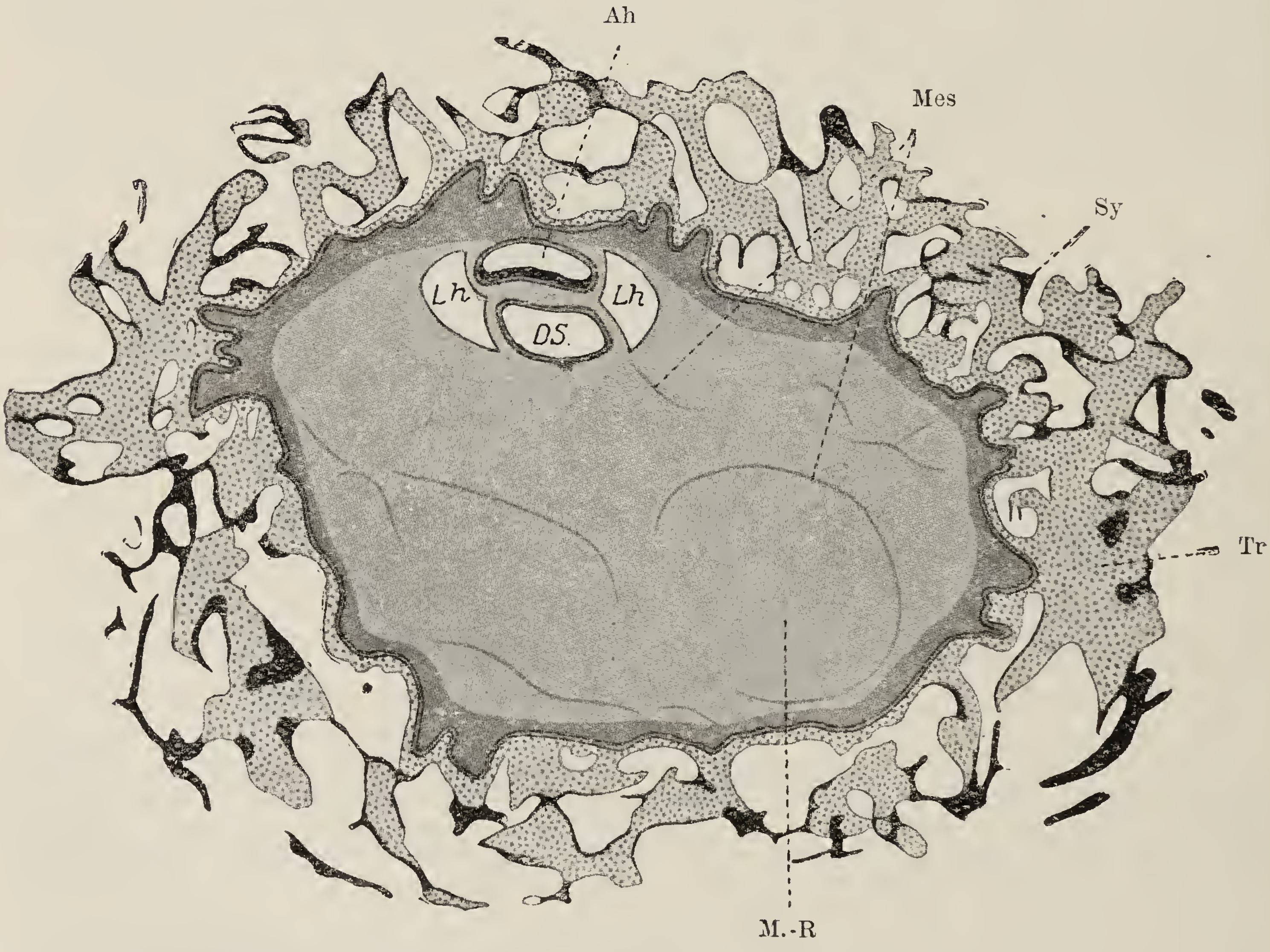

FIG. 54.—Scheme of Peter's ovum according to Grosser (fig. 7). Explanation in the text. Ah = medullary-amniotic cavity; DS = yolk sac; Lh = extra-embryonic cœlom; Mes = mesenchyme; MR = magma reticulare; Tr = trophoblast; Sy = Syncytium of the same (derivative of its upper layer, the plasmoditrophoblast).

are visible. In the latter three cells are differentiated (hypothetical); an upper, which gives rise later to the embryonic ectoderm, a middle, which gives rise to the embryonic entoderm and the yolk sac, and a lower, which gives rise to the extra-embryonic mesoderm. Probably already in the two-celled stage there is found in mammalian segmentation a differentiation of potency (p. 268). Figure 52 illustrates the youngest known human embryo, which was found by von Mollendörff at the site of implantation in the uterus. The figure shows this important stage for our purpose as slightly modified by Grosser. The trophoblast is well developed, and has already extensively invaded the mucous membrane of the uterus. The germinal area shows the knot differentiated into ectodermal and entodermal elements. Extra-embryonically a mesenchymatous mass has extensively developed (so-called reticularis magma). Figure 53 presents the second youngest embryo known (fifteen days old). Within the knot two cavities have formed. The dorsal is the medullary amniotic cavity (cf. figs. 47,d, 48), the lower is the yolk sac. The extra-embryonic mesenchyme fills the cavity of the blastocyst. Figure 54 is the third youngest (eighteen days old) egg, in which the floor of the medullary amniotic cavity already shows the thickened medullary plate. Between it and the yolk sac lies the embryonic mesenchyme. The blastocyst is filled with a mass of jelly-like material, which is derived from the extra-embryonic mesenchyme. Within this mass there has arisen a horseshoe-shaped cavity (Grosser), bounded by endothelium (in the section twice cut), which represents the extra-embryonic cœlom. Figure 55 exhibits a nineteen-day old egg, in longitudinal section, in which have already developed the primitive streak, the

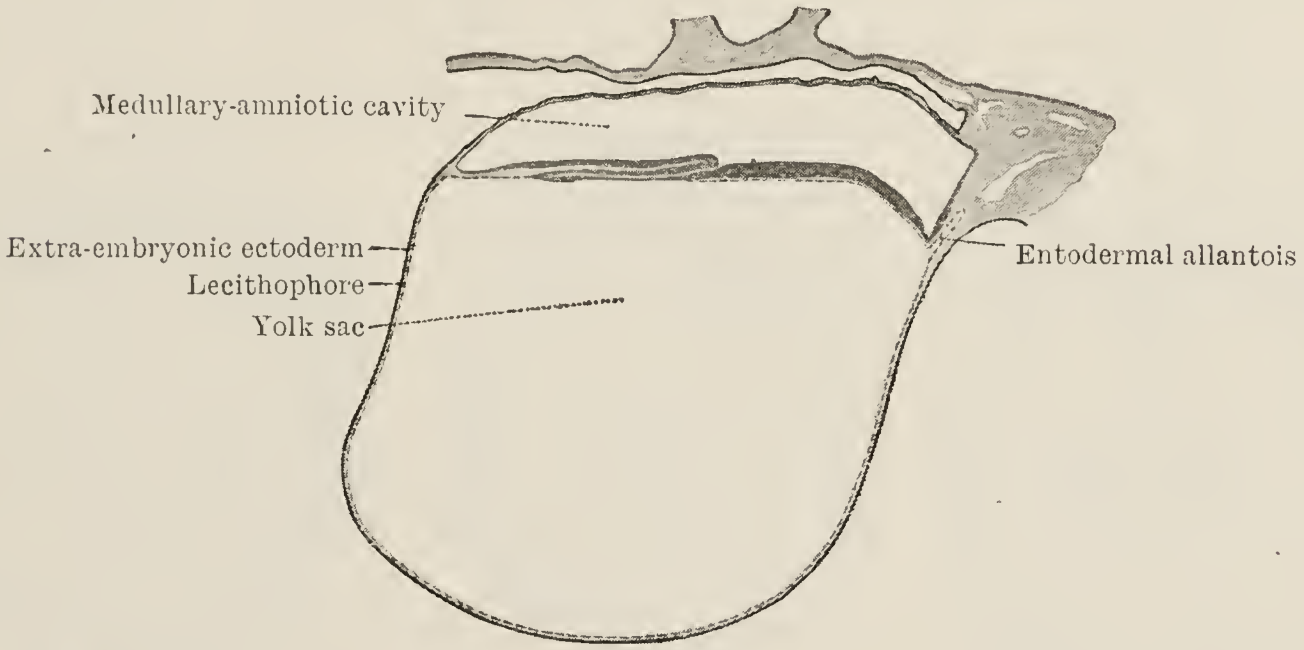

FIG. 55.—Longitudinal section through the ovum of Rossenbek. (Zeitschr. f. Anat. u. Entw. Gesch., Bd. 68, 1923.) Explanation in the text.

chorda canal and head process. The primitive streak lies on the right in the figure. Here the ectoderm and the mesoderm have already fused (peristomal mesoderm), while the entoderm passes smoothly below. In the middle opens the chorda canal, which stretches into the head process. The lower wall of the canal lies on the entoderm. A break through into the yolk sac has not yet occurred (it arises in the region of the attachment). The comparison with fig. 41, *C, D*, teaches that there is perfect agreement as soon as one recalls a yolk sac filled with yolk.

Very remarkable in this and in all human ova at the same stage is the fact, that the process of invagination is so extraordinarily clear, even schematically clear (cf. fig. 41). The human behaves quite primitively like the reptile. At any rate the invagination and its topographical relations can be much more clearly demonstrated than in the bird, and especially in the chick. Very striking, and observed in no other mammal, is the cell mass protruding behind the primitive groove, which lies in the same manner as the yolk granules in a yolk-laden egg. (In fig. 55, in consequence of the marked reduction in reproducing, the figure is only imperfectly visible on the right of the primitive groove.)

Figure 56,a shows clearly schematically the amniotic cavity separated from the trophoblast by the upward growth of the extra-embryonic mesenchyme. The gut is joined to the yolk sac (omphaloenteric canal, Meckel's diverticulum). The allantois has grown out from the hind-gut. The extra-embryonic cœlom has extended on both sides to the allantois. Its bounding layers are the embryonic gut and skin layers, in between which lie streaks of the magma. From the region of the allantois the mesenchyme has developed beneath the trophoblast, so that now the chorion arises in typical fashion from the mesenchyme as the basic layer, and the trophoblast as covering layer. Finally, the primary villi have developed. Figure 56,b shows the continuance of the enlargement of the amnion, the formation of the secondary villi and the separation of the trophoblast into chorion basale (placental side) and chorion læve. Figure 56,c shows the complete development of the human fœtal membranes. The amnion fills the exocœlom almost completely (later completely). In figure 56,c the exocœlom is still visible as a clear space between the amnion and the decidua vera. Ectodermal and entodermal allantois and yolk sac (umbilical vesicle) are pushed together at the umbilical cord by the amnion.

Later the wall of the amnion cavity is formed by amnion and the chorion læve, which includes on its outer side the decidua capsularis;

these fuse with the decidua parietalis (vera), so that in man the uterine cavity becomes perfectly obliterated.

Para. 83. If we summarize the described processes we can see that they can be fitted without difficulty into the mammalian development, and generally, according to the views already expressed [para. 78], indirectly into the fundamental processes of early development. For the formation of the neurula is expressed quite clearly in figure 55. For the processes before the formation of the primitive streak agreement exists on the following points :—

(1) Segmentation and formation of the blastocyst are very close to the processes in the field mouse (figs. 47 and 48).

(2) The trophoblast shows clearly the formation of cyto- and plasmodial-trophoblast. Both play different parts in the embedding of the egg in the uterine wall. They persist (after many changes) in the placenta as the cellular (Langhans' layer) and the syncytial (syncytium) portions of the chorionic villi (fig. 54).

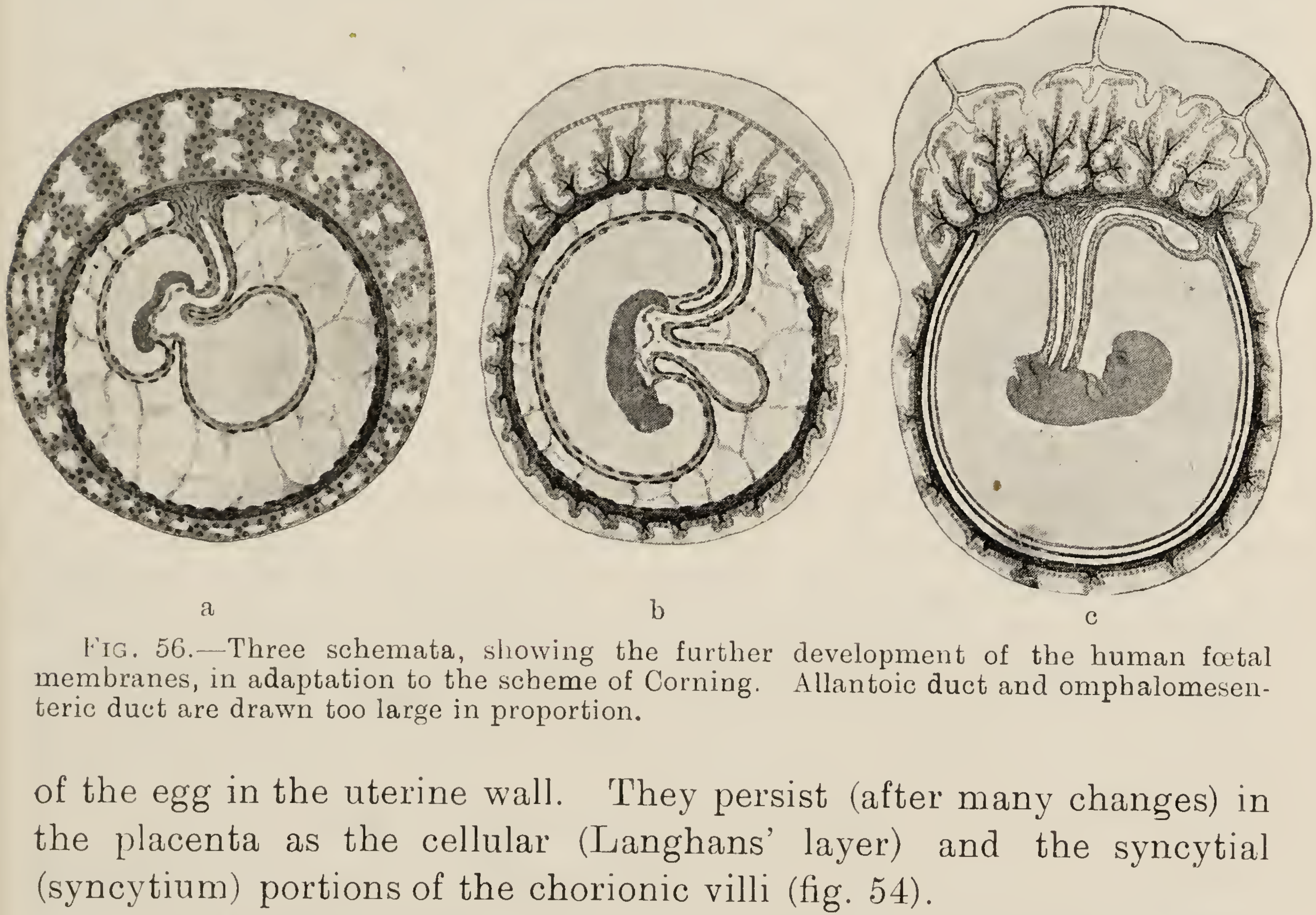
a b c

FIG. 56.—Three schemata, showing the further development of the human fœtal membranes, in adaptation to the scheme of Corning. Allantoic duct and omphalomesenteric duct are drawn too large in proportion.

(3) The allantois shows the typical relations for the early implantation of the egg in the uterine wall, slight capacity of the entodermal vesicle, massive development of the mesenchyme. The mesenchyme extends below the trophoblast and forms the basis of the secondary villi with the branches of the umbilical circulation.

In addition there are some processes peculiar to the human egg which make its early development unique (it may be that they are also present in the remaining primates, but this we do not know). We begin with the subsidiary forms :—

(1) The smallness of the yolk sac. Whilst in the mammal the cells of the lecithophors (cænogenetic entoderm) extend right under the trophoblast, they are pushed together in the human egg so as to form a small vesicle; therefore follows:—

(2) That the blastocyst persists beside the yolk sac. This cavity is filled with mesenchyme, a condition until now unknown.

The tissue in the beginning arises from cells with processes and fibres (v. Mollendörff), later (Grosser) more from coagulated flakes, which are only traversed by individual cells. It lies not only around the embryo, but also between the ectoderm and the entoderm in the region of the shield (embryonic mesoderm, fig. 54). In the further development this tissue (also called the magma reticularis) fuses more and more, and only stops where the allantois meets the wall of the germinal area (figs. 55, 56,a). If the magma is destroyed then the cavity corresponds to the exocœlom, which has already risen earlier beside the embryo. This extra-embryonic cœlom is, as everywhere, composed of two layers. The outer lines the inner surface of the trophoblast and the inner the surface of the amnion and the yolk sac (fig. 43). The conjunction of the amnion yolk sac and serous membrane in this remarkable manner is here demonstrated (figs. 43, 45, 49,a). It brings out the force which lies at the bottom of these structural formative processes, but also shows the plasticity of the means which the organism possesses. As always the inner surface of the yolk sac is placed in the splanchnopleure, the outer of the amnion comes into the somatopleure at the umbilical orifice of the embryo. Both layers are present, where the allantois meets the trophoblast, and fused together. Here the magma tends to persist as mesenchyme (fig. 56).

The morphological significance of the extra-embryonic mesenchyme and the establishment of the exocœlom in it are as yet in no way explained. It is, moreover, important that this mesenchymatous structure arises before there is any far-reaching differentiation of the embryo. This has hitherto been known in no other vertebrate. It follows, therefore, that the human egg in the earliest segmentation phases proceeds, as it does in the eggs of other animals, to a qualitative differentation of the dividing cells. At an early stage the mesoderm-forming cells are differentiated among the dividing cells lying in the interior. Hence the schemes of figs. 51,b and 51,c. It is in the highest degree significant that at so early a stage of development there should be this differentiation of the lines of cell development, principally of mesoderm-forming cells, for this quite generally happens in the invertebrates. The next time we meet it is in the highest living form where we can assume it with such certainty, though unfortunately hitherto we have not been able to prove it.

Perhaps the explanation of this can be found in a morphological principle. As we ascend, the formation of (cænogenesis, pp. 262, 322), the extra-embryonic mesoderm in the amniotes predominates, and we see it perfected, and therefore we must (para. 81) bring this into relation with the allantoic development. It is correct to accept this in mammals and man, because here is found a great increase in its functional capacity, owing to the great functional importance of the allantois for the formation of the placenta. So then, in a functional view, we can adopt the idea (Grosser) that the blastocyst is used for the accumulation of embryonic nutriment, which arises from the early implantation of the egg and the collection of dissolved tissue from the trophoblast, before the embryo, which grows for a very long time, can use this nutriment. The jelly-like magma has this semi-digested embryotrophe to thank for its existence. In the smallness of the yolk sac (morphological) the blastocyst filled by magma might be a physiological yolk sac.

(3) The primitive magma persists as the investment of the allantois. In consequence, the spread of the exocœlom between the allantois and the posterior pole of the amnion is suppressed. In order to present the typical arrangement the allantois must be "removed" from the amnion at this point through the ingrowth of the exocœlom. This, however, is suppressed. So arises a stalk, invested by mesodermal epithelium, which runs from the belly surface of the embryo to the trophoblast, the body stalk (so called because it is a provisional umbilical cord; it becomes later the definitive umbilical cord), a formation which is observed also in other primates. The place where the body stalk meets the trophoblast is the site of the placenta (fig. 56).

(4) Finally, in the development of man (and anthropoids?) the gigantic extent of the amniotic cavity is overwhelming. It is this which in further development completely suppresses the exocœlom (fig. 56,c). For the subsidiary organs it has this consequence, that the umbilical vesicle and body stalk are always pressed closer together and finally are contained in a cord covered by the amnion.

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(B) Experimental Analysis of the Developmental Processes.

(1) Introduction; their purpose.

Para. 84. Our short sketch of the formative processes has attempted to portray what occurs during development. Since we observe the results of changes passing before us the question presents itself as to the why and wherefore of these changes. It is clear from what has been said before [para. 32] that these questions in themselves admit of no answer, since the answer can only lead to this : The inherited constitution of the fertilized egg is the cause of its behaviour during development. The question of the wherefore of the individual ontogeny is bound up with the question of the genetics of the formation of specific cells. However, the individual phenomenon in its invisible complication is composed again of numerous steps, each of which is necessary in the course of the whole. The possibility arises here of a question which differs from that of genetics. It is admitted that all the innumerable steps march together according to the laws of the inherited constitution, yet each individual step in itself is in relation with all the preceding and contemporary conditions, that is, it is defined according to time, place, direction, quality and quantity. This necessary definition is only recognized as lawful when it can be exerted on a complete causal portion. If we only describe an individual developmental process, then we only deal with the associated effect of this partial cause which fails in the inorganic world, as does the internal subdivision in the organic world. To investigate the partial cause of the phenomenon and its effects, the observer must regard the purpose of living things; it becomes the problem of experimental embryology. Experimental embryology ought to determine the factors by which a definite constitution will necessarily express itself in space and investigate the manner of their working [cf. para. 92, conclusion].

The older natural philosophy had, under the implications of preformation, to recognize the ontogenetic phenomena as necessary, since the acceptance of a preformation implied the presence in the germ, in minute or invisible manner, of the same diversity which the later object afforded in a more visible manner. Epigenesis, on the basis of the first exact investigations into embryology (K. F. Wolf, Pander), represents development as a continuous process, and does not find this diversity in the germ. The germ appears as something simple. The diversity arises through a series of new formations, and the attainment of this diversity lies in the actual development. We know now that the starting point of this development is not the obvious simplicity of the old epigeneticists, and that diversity may be present, even if it is imperceptible. So we must take our starting point from a preformation which ought only to be spoken of as a " neopreformation," that the germ possesses a specific structure and form, exhibits a whole, differentiated within itself, which serves the inheritance of the organization. Granted these things, it is yet not possible to say how far the development runs an epigenetic course (the establishment of new complexities) or runs an evolutionary course (the unfolding of the diversities already present). Many would say that a complicated state, yet proportionately simple, forms the starting point in which further new complexities arise (neo-epigenesis). These are distinct from the original make up. In place of the older theories, with their catch-words, preformation or epigenesis, there is now an intelligible and easily understood scepticism. This has led to many results without having established any one theory of the development of organism [para. 92]. This is no defect, but only natural in the light of all organic processes.

This explanation was necessary in order to proceed to a discussion of the partial cause. In the most recent sense complexity indicates a muliplicity of partial causes. Perfect preformation is established if all partial causes of ontogeny were actually present from the beginning.

In the causal investigation all the phenomena are divided into partial causes and partial effects, and the development is investigated where relations between the formative processes arise in various organs. This implies a different conception of the phenomena of causality. It corresponds therefore to causal relationship [para. 9]. This is not to imply that there is another form of causality, but to emphasize that not only the form of the end-products from a definite starting point, but also the form of the individual parts stand in an ordered necessary dependence on one another. Following the same plan as before [para. 21], we speak more fully of the systematic characters. Here we need only concern ourselves with the systematic characters of ontogeny.

Since now the normal phenomena can no longer stand fast as definite stages, the investigation, if it would actually prove the partial causes, must analyse the conditions under which a definite stage issues from a preceding one. The means to do this are found in the artificial influencing of a given individual ontogeny. The analytic embryological experiment analyses the stage of the development in order to establish its cause.

The assumptions are of quite a special form in regard to the object and to the ideas. There is in the one case a series of stages of a developmental process starting from a historical necessity and leading to the unfolding of the structures of an organism; a spatial arrangement of individual parts changing in sequence, parts growing and parts fully functioning lying side by side; in the other case an interference causing a destruction of the whole condition. The result must always be a reaction of the injured system to the injury. What the experiment shows fundamentally is the reaction of a historical system, growing, and at the same time unfolding, to an injury. Experimental embryology in the analysis of its results has this object, viz., from the type of reaction aroused through an intentional injury to draw conclusions on the phenomena of the behaviour thus affected. This is not always appreciated. It is replaced by the assumption: the reaction produces effect, an uncritical use of the method which does great harm to the validity of the results as is easy to see, and will later be further exposed.

(2) Introduction to the Concepts of Experimental Embryology.

Determination, Differentiation, Potency, Regulation.

Para. 85. When complexities arise in the embryonic development these phenomena must be at each moment the resultant of all the conditions under which the causes are at work. These conditions are internal and external. The external world presents them, but also the internal environment, since the parts are connected to one another by subtle relations. The parts are often—but not always—dependent on one another.

This dependence is described as correlation, when it rests on essential effects between sharply defined morphological parts under the influence of formative stimuli (for example, development of the central nervous system only in the presence of bone and, conversely, development of bone only in the presence of an intact nervous system in the frog). It is called relation when there is a one-sided dependence of a sharply defined morphological part on a formative stimulus (for example, the lens of many amphibia is dependent in its formation on the presence of the optic vesicle, but not conversely—this is a very important distinction between correlation and relation according to Dürken).

This dependence we can estimate in two ways, from the standpoint of what is present at the beginning and its mode of growth, and from the standpoint of the end-product, which exhibits its complexity. From each standpoint we proceed to the idea of determination and from this to the idea of differentiation.

Determination is, in essentials, like preformation in the germ, the totality of all the factors in the fertilized egg which determine the development, "complex of determining factors."

In the sense of neo-formation it is the whole of the structures subserving the inheritance and form of the germ. With continued development the complexity will disclose itself as the whole complex of determining factors in an unending series of individual complexes of lower form.

A dividing cell of the four-celled stage is determined to form its daughter cells, and therewith the whole of its subsequent history. The whole of the ectodermal cells will possess at various points different determinations: one to form the medullary plate, another for the formation of hair, of glands. The cells of the medullary plate are determined for the formation of nerve cells and neuroglia. The mesenchymatous rudiment of an extremity in its totality is determined for the formation of bone, muscle, vessels and, perhaps, nerve. If the determination is further localized within the mesenchyme cells, so that only definite cells are determined for the formation of the skeleton, and if this determination expresses itself in some way, the observation of the ordinary phenomena enables us in no way to arrive at a decision. Only by experiment can anything be ascertained on these points, as for example, if the cells of the medullary plate under artificial conditions form something else related to mesenchyme, such as the somites. The determination would, looking at the end-product, be very far-reaching but not the sole factor; if the experiment resulted otherwise and a medullary tube was formed at all points, then the determination would be conclusive; to this condition the name "destination" has been applied (Graper).

This demonstration of determination in itself affords only a partial explanation of the phenomena. Something else is necessary, a push, a stimulus, a drive, a release [para. 21].

These necessary factors of development are put as realization factors beside the determining factors. While the determining factors lie in the cell as well as in the rudiment, the realization factors are brought into play by the influence of the surroundings, and also through the influence of one part of the body on another. Thus, if the development of one organ is necessary to enable some other to arise (for example, the optic cup, in order to bring the lens into being). The determining factors of a form are the essential specific ones which determine the quality of the appearance; the realization factors are the indifferent stimuli (thermal, chemical, position, etc.).

Under normal conditions the determinant is invisible. Its presence is not detectable but it becomes obvious in its results. This determination which becomes obvious in its results is differentiation. From the standpoint of experimental embryology differentiation is change of form.

What is the relation between determination and differentiation? Is there a determined rudiment which is not yet differentiated, and is there differentiated material which is not yet determined? The first is generally accepted. It cannot be certainly proven, since our optical instruments are incapable of making visible the finest form of the cells. It is certain that differentiation occurs very much earlier than it appears to us.

So we know that within the perfectly indifferent mensenchyme of an extremity rudiment cells are already determined which form the later cartilaginous skeleton (Braus). The converse that something is differentiated without being determined definitely under normal conditions occurs not so seldom, for example, when some cells of a highly differentiated sense-epithelium return to their epithelial form, and through their increase a single layer divides into two; or when cells of outer root sheath of the hair increase and form a new hair bulb. Also in the secretory cells of the gland acini a similar differentiation occurs. Experiment shows such cases extraordinarily frequent. What is differentiated as the rudiment of the spinal cord can form a transplanted primitive vertebra; the striatum corneum of the epidermis can become epidermis around an extremity bud transplanted within it while the epidermis of the transplant becomes mesoderm. Pathological observations show that tissues which appear most highly differentiated are not finally determined. The most remarkable example of this kind of thing has only recently been observed. The small intestine when used to form an artificial anus takes on the structure of the large intestine. In all the cases investigated there is either a de-differentiation or a still further differentiation.

The extent of the determination and the degree of differentiation therefore often correspond, but not absolutely. The differentiation of the material creates this new situation within the developing germ, so that new complications arise and these introduce new determining factors, and so the complexity increases. As soon as the neural tube and the primitive vertrebræ are differentiated new relations arise which are determinants for the development of the nervous system. As soon as the formative material for the skeleton is differentiated between the chorda and myotomes important relations arise between the two which affect the divisions of the vertebræ and determine the invertebral discs.

If the primordium bears all its determinant factors within itself, it must form its different structures under the influence of indifferent stimulation factors only. One speaks, therefore, of self-differentiation. In a real sense, it is never absolutely present, since all developing primordia stand in relation with one another and in some degree dependent on one another. Their presence, of course, can only be determined by experiment. If, for example, the primordium of the eye be transplanted in the abdomen it still forms an eye; if a left extremity be transplanted on the right side it still forms a left extremity. Therefore, one speaks in general of self differentiation. Dependent differentiation arises on the contrary when the unfolding of indifferent material can only occur under the influence of another organ, a primordium, in its neighbourhood. We should consider, for instance, that the differentiation of the trunk depends on (not caused by) the presence of the dorsal lip of the blastopore.

The question of the nature of this dependence and the means by which one differentiating primordium affects another is still open. It appears as if distant effects play no small part herein (chemical, electrical emanations of some form). Recently (p. 44) the places were described where such effects might begin as organizers (Spemann and Mangold, v. Ubisch). They were, for instance, the dorsal lip of the blastopore, the primitive knot of the chick (Wetzel), the roof of the archenteron (Spemann, v. Ubisch). One must be very careful in passing judgment on these ideas. It would be valuable if one could submit the embryo to a crucial experiment. Already a slightly closer acquaintance with the questions that depend on the relations of "organizers" has shown (Spemann, 1924) that it is dependent on its own capacity for organization and on the effects of the surroundings. One can therefore go so far as to say that what in itself is first differentiated through an "organizer" (for example, the material of the trunk ectoderm, which is organized into a medullary plate by the entoderm) can in its turn become the "organizer" if one brings it into the position of the entoderm in the interior of the gastrula. All these investigations move in a circle and only suffice to show that dependence finally arises in diverse ways. The irrationality lies not in the infinite complexity but in the mode of organization generally, which we can comprehend scientifically only in parts.

Para. 86. From the ideas of determination and differentiation one proceeds to the idea of potency when one attributes the development of a cell to a formative tendency and from the standpoint of cellular intelligence judges its formative differentiation as such a tendency. We declare then that cells, tissues, primordia have the power to form structures. This "general endowment of the power to develop" is described as potency. It is a general potency since it involves these three things: (1) Potency for self differentiation; (2) power to influence the differentiation of other structures, that is, to determine dependent differentiation; (3) power to undergo dependent differentiation.

The typical phenomena here are rather unsatisfactory in bringing us to the real kernel of the idea of potency. We are not concerned with what a primordium actually does, which we can observe anywhere in development, but rather with what it can do. This is, however, visible only in non-typical development, in abnormalities and monstrosities. We think of the variation in the course of arteries, hermaphrodites, and twins, complicated fissure formation in the brain, six fingers, and many others.

From such cases we must conclude that the potentialities of the primordium are greater than ordinary development would lead us to suppose. Thus, a dividing cell which normally only forms one half the body may, under other conditions, give rise to the whole body (homologous twins). Only the disturbed development induced by experiment has shown that in general the most extensive potency does not lie in the normal end-product. A primordium which is normal to the brain can form something quite different under certain conditions of implantation. If a dividing cell be isolated, instead of forming a portion of the body as it would if it remained united, it now forms the whole body, only much reduced in size. If an arm is removed from a triton larva young cells form at the cut surface, and these regenerate the whole of the lost member. These cells which were "determined" in the normal state, forming after section only the humerus, the arm musculature, etc., have in a roundabout way provided something quite different from an indifferent cell form.

So there is the necessity to distinguish between what the cells can do (potency) and what they usually do (significance). Both qualities have been indicated by the word "prospective." The terms prospective potency and prospective significance have been adopted though the double use of prospective is either unnecessary or false (Graper). The double implication arises since one can imply it, and has actually implied it in the expression "foreseen by the cell intelligence"; unnecessary, because prospective potency can only mean potency in the future and its realization naturally only comes in the future, i.e., can only be manifested in the course of the phenomena. False, finally, because the "significance," which one can only determine when the development is at an end, beside not being prospective, is on the contrary our retrospective interpretation (Graper). So we will only speak of the potency and significance of cells, tissues, primordia, etc. In this respect the normal appearances must find a place in order to make intelligible the facts of determination and differentiation, the ideas of loss of potency, and of the limitations of potency. The potency of the fertilized egg is that which gives rise to the whole body. The potency of the segmenting cells of ectoderm to form epidermis, hair, etc., becomes continually smaller. The increasing differentiation of the whole goes hand-in-hand with diminishing potency. Highest differentiation, final destination, and most limited potency are equivalent ideas (for example, a liver cell). So one can speak of toti-, multi-, and unipotency.

There are clearly here adumbrations of the conceptions of genotype and phænotype. What the geneticist describes as genotype is the potency of experimental embryology; and what is phænotype for him is, here, the significance (Peterson). The small intestine of man is phænotypical intestine (significance). Genotypical is something different (potency, the power to form the mucous membrane of the large intestine, perhaps many others which we do not know).

This brings us finally to the problem of how we are to think of the process of the limitation of potency. Is the potency diminished and only a little or a part expressed? Or does it wholly or in great part remain, but through some unrecognizable (chemical) neutralizing process become inactive and achieve nothing? At the moment we do not know which is the case. Many processes in heredity and the fact that primordia in abnormal development unfold other potencies than in normal development suggest the latter alternative. This question is in the same obscurity as that of the like or unlike inheritance of cell division (pp. 315 and 361).

From the fact that a primordium develops into a different form in abnormal development than in normal, and becomes dissimilar through this abnormality, one is forced to the far-reaching conception that the capacity of regulation (formulation) applies to cells and primordia (self-regulation, p. 35). This implies the activation of potencies by which an abnormality can be produced. This affords the possibility of such differentiations which would have been occasioned by other cell connections.

If a cell mass be removed from the primordium of an extremity and be transplanted to some other place it is known that, in amphibia, from this transplant, an extremity with a normal but reduced shoulder girdle arises, though these mesenchyme cells in their normal position could have produced only a part of the shoulder-girdle. It has already been mentioned that the limb bud of the left side, if transplanted to the right, forms a right extremity.

The embryonic cells and cellular primordia have been described as "equipotential systems," since, by experiment, their regulation capacity has been generally demonstrated. By this, one means that there is present an active regulated cell-complex in which "each cell can replace the other" if brought under corresponding conditions. One might go so far as to see in this a fundamental peculiarity of all living beings, that their bodies may be a harmonious equipotential system. Let us now see if and how far we are correct in this conception and if living things actually possess this peculiarity which would distinguish them from the inorganic world. In pure dynamic (not morphological) terms, we might go so far as to recognize "self regulation" as the guiding principle of all living processes, with the result of self preservation as the chief characteristic of life [para. 13].

(3) The Methods of Experimental Embryology, Exposition and Criticism.

(a) Presentation.

Para. 87. In contradistinction to the type of experiment which has been in vogue more than a hundred years, an experiment in which one only changed the living state without knowing what was changed in the interior of the organisms thus influenced, the analytic experiment works by means of a planned operation at a definite point at a definite time, changing a single partial cause (a factor), not an obvious combination of partial causes and effects, in order to observe the normal ontogeny. Experimental embryology feels itself on safe ground on the basis of the consideration that all the factors of a phenomenon are necessarily the same and that they cannot be interchanged (equal necessity, invariability of the factors). Thus, according to the theory of experimental embryology, a single factor may be changed and the effect of this change observed and appreciated. The experiment starts from the point of placing the developing organism in the position where it is compelled to answer a definite question. One chooses a definite stage in the development in order to extort the answer.

The type of inquiry arises from this. It can be systematically arranged as follows (Schaxel):—

(1) Removal of parts. A cell or a group of cells (primordium) is so influenced that it plays no part in the furthur development, e.g., through death by mechanical, chemical, thermal, radio-active means. The excluded part remains in connection with the organism.

(2) Transposition. By weight, pressure, agitation, parts are brought into positions they do not normally occupy. For example, a frog's egg is placed with the vegetative pole towards the exterior, fixed there, and development allowed to proceed; the cells of the frog at the morula stage are brought under a compression in one plane and their development observed in the new position.

(3) Excision. A part is removed completely from the organism. A divided cell is separated. What happens to the cell which is left? What happens to the separated cell? Primordia and organs are removed. What happens in the place from which they are removed? This last is the starting point for a special method which investigates isolated tissues in nutrient fluids outside the body (explantation).

(4) Grafting. A new system is implanted in the organism. Transplantation; implantation of organs and primordia.

(5) Compensation. In the place of an organ or of a rudiment another organ or rudiment is implanted.

As the object of these inquiries every stage of the development may be used—the fertilized egg, segmentation stage, stages of primitive development, stages of tissue and organ formation, later embryonic stages, fœtal and adult organisms.

Para. 88. Anything approaching an exhaustive criticism of experimental embryology lies far beyond the purpose which we have in view. We will only give a survey of the more significant experiments which have been performed. In this series we will take experiments which have been applied during development and have often been mentioned.

(1) Inquiries on the fertilized egg. Eggs of many invertebrate animals after destruction of part of their protoplasm show widespread malformation. Later tissues and organs fail to develop. The protoplasm has the power no longer to repair the defect. In the protoplasm of the egg therefore the later organ regions lie spatially separated from one another exactly as they had been represented in the old doctrine of preformation (mosaic theory.) In the eggs of other invertebrates and the eggs of vertebrates, possibly with the exception of mammals [para. 83], it is otherwise. Here a defect can be restored, for the protoplasm has the power of compensating, because the primordia are all here arranged in the same manner (regulation eggs). If the defect or the injury be very severe, the constitution of the egg is profoundly affected, and no compensation is possible (Schaxel), it develops abnormally ; there is a transition between the regulated egg and the mosaic egg. The result of these experiments is this : the egg protoplasm is either differentiated as mosaic or it is not. Instances exist where the primordia are indifferently distributed through the whole of the egg protoplasm (the protoplasm is therefore not differentiated). Others are found in which the primordia are specially arranged. Alteration in the position of the egg substances by the application of pressure or defect in the plasma can in the last-named instances be compensated, but only when the determinants for the specific structures have not been destroyed. In the mosaic egg this compensation can only occur with difficulty and in the most highly mosaic differentiated egg cannot occur at all.

(2) (*a*) Inquiry into segmentation. Destruction of a cell, though retaining its position, preventing further development. The untouched cell provides a half embryo (frog's egg, Roux, 1888). This experiment is of historical significance since it was the starting point of the whole of experimental embryology. One has (p. 172) —neglecting the value of the question of potency—regarded the result as proving that the first division divides the material into right and left. This, however, is certainly not correct, since the plane of the first division arises in the frog (different in other eggs) in a plane quite different from that of the later plane of symmetry. The two cells of the first division may possess the material for each half of the body but do not always do so Most contain material for both sides of the later form and none the material entirely for one side: The experiment proves, therefore, that each cell has the potency, though not the entire material, of its side, to form through regulation the missing material whenever it is separated from the other cell. Also the destroyed or damaged cell can form one half of the embryo in which material of the healthy side, or material yet living perhaps

of the damaged cells, is used. This " post-generation " is the most favourable example of a dependent differentiation, namely, that of the complete half-embryo by the healthy side.

(*b*) Separation of the two cells by a constriction. Result: From each cell arises a complete embryo or twins.

(*c*) Isolation of the dividing cells. Perfect isolation of the cells of the first division from one another (amphioxus, rana, sea urchin) produces from each cell a complete embryo but of half the size. Constriction of the two-celled stage by a thread along the plane of division (triton, Spemann) produces the formation of two larvæ of half the normal size. Imperfect constriction in this plane produces twins. They, for example, may fuse in the tail region. Isolation at the four-, eight-, and sixteen-cell stage (sea urchin) produces a very small organism. At the more numerous cell stages the isolated cell produces only a blastula as an end-product. Any later development is defective. Isolation from the four-cell stage (amphioxus) of a single cell, produces from this cell a very tiny form; isolation at a later stage leads only to defective development. In the axolotl, isolation at the two-celled stage leads to the formation of a perfect form. In the later stages the isolated cell produces only a morula. The defects follow. At the point from which the isolated cell is taken defects arise.

These observations afford perhaps the explanation of single egg twins (p. 174). They throw some light on the questions of potency, regulation and determination. The first two cells are determined in opposite directions, though each can form a whole embryo, yet forms only half the body (separation experiment). In the isolation experiments distribution of the protoplasm arises through regulation, so that each cell forms more than it normally does. This so-called " regulation ability " is specific and not general and depends on the length of time the whole constitution of the egg, " qualitative, quantitative and proportionately equal," can be transferred to the daughter cells. It seems to disappear in the four-celled stage (sea urchin), in the two-celled stage (amphioxus), or exist only in the first division (axolotl). If one calls these eggs generally " regulation eggs " of the fourth, third, second, and first stages, then the mosaic eggs mentioned above are without this regulation process. They belong to the " none " stage of the series. The above-mentioned series is again present in so far as many eggs can form a part of the organs entirely from the dividing cells, i.e., in relation to the whole animal. Parts can be formed many times, while others have not this power. The reason cannot be that the dividing cells possess a general " regulation capacity." Along with the successive divisions (from the first, second, third, fourth series) there occurs a progressive diminution of this potency. This diminution of potency is not shown by abnormal development but in the fact that only some primitive stage of development is reached (morula, gastrula), and there the development stops. The material cannot reach any further stage of development. The same appears in the rudiments of the organs (see later reference to the shoulder-joint). A series of excision experiments demonstrates the sort of thing that happens. A fusion of two cells (amphioxus, Strassen) or of two two-celled stages (triton, Spemann) produces a single giant organism. Here a limitation of potency arises from the proximity of the partners; the cells produce less than they do normally. The power of regulation and the converse, determination, are hereby demonstrated (dependent differentiation).

(3) Inquiry into the primordium-complex. (Primordium = the precusor mass that subsequently differentiates into a recognizable tissue or organ.) (*a*) Excision experiments in a pure form have scarcely ever been brought off. One of importance is as follows: The development of the premuscle mass of the fin of a dog-fish was suppressed (Braus). The development of the skeleton proceeded as usual. This development, however, only reached its normal condition if the whole of the material for the development of the skeleton was present. If this mass was destroyed, then only the cranial part of the skeleton of the fin was properly developed. The first primordium of the skeleton appeared through self-differentiation; within the primordium-complex the differentiation of the cranial part released the caudal part. The process of self-differentiation undergoes a reduction distally (dependent differentiation within a primordium that arises on the whole by a process of self-differentiation).

(*b*) Transposition experiments. Larvæ of amphibiæ were halved, and parts of different individuals of the same or different species grafted on (Born). The results are very complicated and various, but essentially they show that the individual parts either (in favourable situations) grow to organs or take on a special development of their own (self-differentiation). There are striking differences in the individual parts. Such, in which the primordium is fundamentally self-differentiated, are favourable for this sort of experiment; others are unfavourable because in them the dependence on one another of the components of the development is very great. Similar investigations in earth-worms showed that individual organs do thus arise (direction stimulus for growth).

Investigations on the determination and differentiation of right and left, anterior and posterior, upper and lower, have been carried out on the extremities. In amphibian larvæ the extremities at various stages of development have been transplanted from one to the other side and rotated in different ways. Results: Transformation of a right primordium into a left is possible for a time. The primordia do not possess within themselves all the factors necessary for their differentiation. Later this capacity which permits of transformation becomes reduced. The time when this transformation capacity disappears differs in different species (Brandt). The determination first arises gradually, and for the different axes of the extremity (proximo-distal, dorso-ventral, latero-medial) at different times. The behaviour of the otocyst is similar (tadpole). This follows its development irrespective of where it is implanted. The right brought to the left remains a right; it contains, therefore, all the factors necessary for its development as a right organ, and the direction stimulus within itself. Fusion together of two left half bodies, so that the new right half has its ventral surface uppermost. Here arose from the yet indifferent cells of the ventral surface a part of the medullary tube. The blastopore becomes completed by the normal dorsal side; from here arises the formation of the medullary plate. A portion of the medullary plate in the region of the rudiment of the eye was rotated through 180°; the rotated portion followed its normal development undisturbed, so that parts of the brain were arranged in the reverse order (fore-brain, mid-brain and diencephalon). Result: Already the cells of the medullary plate have their final bias before their differentiation becomes obvious.

The eye primordium, halved by the experiment, is doubled on each side; in front a complete optic cup, but behind incomplete. In this experiment healing was complete though there were local differences; ventral skin grew at the gastrula stage instead of dorsal skin, and this provided a medullary tube, even when it was rotated through 180°. Here dependent differentiations are therefore found in a material not yet fully determined. In the region of the gills the ectoderm was removed from its visible rudiment, and, from other tadpoles of the same size, taken from the same place and twisted through 180°; and in place of the gill ectoderm, ectoderm from other places on the body was transplanted. Result: Only the gill ectoderm had within itself the capacity to form gills; it unfolded this capacity without any stimulus from the entoderm, but, of course, depended on the functional growth of the blood-vessels. The taste buds arise independently of the ectoderm. For the formation of the slits contact between ectoderm and entoderm is necessary.

Here also belong the lens experiments. The formation of the lens does not occur if the optic cup be removed in some but not in all amphibian embryos. An optic cup transplanted at some other point of the body excites lens formation in the neighbouring ectoderm (not in all investigated species). The formation of the lens appears according to the species as an independent or dependent process. More searching experiments have shown that by special temperature effects lens formation can be excited in every case (v. Ubisch).

(*c*) Removal of the primodium. This has been mostly studied along with its transplantation. If an organ that has been removed grows again, then experience has shown that some remnant has been left behind. Complete removal of the primordium (head, eyes, gills, tail, extremities) is not compensated in the axolotl (Schaxel). At the place from which it is removed, only destruction of a local nature appears; the removal of the organ does not lead to any subsequent injurious effects. Similar results follow the complete removal of organs in the tadpole. The primordium of the eye is not compensated in the frog. On the contrary the primordium of the eye in the triton embryo is regenerated from the upper margin of the iris (this does not happen in other amphibian embryos) and also from the inner surface of the retina. If in an extirpation, for example, of the primordium of the extremities, some cellular remnants be left, these provide according to their extent perfect or imperfect limbs. In investigations on tadpoles and turtle embryos so much may be left behind that an imperfect shoulder-girdle arises. In the turtle embryos no regulation is found. The result is the same as if one had cut out a part of a perfect shoulder girdle; the remains of the rudiment do not behave as if they were going to form the whole of the shoulder-girdle. It is just the same as happens in the sea-urchin's egg at the fourth division stage, when the isolated cell only goes as far as the complete formation of a gastrula, where it stops. The cell material was obviously distributed, qualitatively and irregularly (Braus). The cut-out portion did not produce the complement of this defect, but produced a perfect shoulder-girdle in miniature (Ders). The cells in the immediate neighbourhood of the removal, whose destiny is quite different, behave themselves if implanted in another place as a so-called harmonic equipotential system, that is, the primordium cells have now the power to produce something to which they did not attain in their normal position. Free extremities develop normally in the new position.

Implanted primordia need, however, in order to devlop in a new position, to fuse with the underlying tissues; without nutriment they die. Without nervous stimuli they degenerate or they develop normally until the time of function, and then they become stunted. The nerve stimuli can arise from any nerves, e.g., from a branch of the trigeminus which grows into the primordium of an extremity implanted in the orbit. The ingrowth of the nerve in a tissue, either nerve-free or made nerve-free, exerts some regulating influence whose nature is quite obscure, though the nerve is used as its path. If two parts of an amphibian embryo are joined head to tail, so as to form one animal before the nervus lateralis of the vagus arises, the nerve grows into the posterior portion into its normal place from the ganglion of the vagus in its anterior portion (Harrison). What influence determines this is unknown, probably the determining factors lie in the lateral line system itself.

The implanted part affects the surrounding tissues and these in their turn affect the implanted tissue. If an extremity bud be implanted in the orbit we have seen that its own ectoderm becomes mesenchyme, while the stratum corneum of the orbit becomes the epithelium of the bud. Conversely one can in amphibian embryos, through the introduction of the rudiment of the eye or for that matter mere fragments of the eye or lens rudiment under the skin, occasion in these places changes which give rise to a thin horn-like membrane. The red pigmented abdominal wall of the triton becomes darkly stained if a dark-coloured regenerating limb bud be implanted in it (Taube). Further examples of this sort of thing are present in the work of Dürken, p. 208. Examples in which the host is influenced by the transplant are few but do occur (Dürken, p. 224). Those cases are very instructive in which portions which have been artificially joined pursue their own development independently. A bit of the tail is grafted on to the tail of a differently coloured frog. Both retain their own colour unchanged. The compositions achieved by v. Schaxel of the extremities of black and white axolotl larvæ establish for the animal kingdom a perfect parallelism with the "chimæra" of the plants. Compositions of the cells of solanaceæ (nightshade and tomato) provide a growth which show the tissues of both plants intermingled in all their parts. In general, these investigations, of which only a few examples are given from the great number available, illustrate the dominance of the self-regulation of the rudiment joined to numerous influences from the new surroundings; further, they show the extraordinary differences in the results obtained in different species of animals submitted to the experiments. Generalization of results obtained from the investigation of one animal are not at all valid.

(*d*) Inquiries in older animals. Here we may present briefly the large field of regeneration, since it stands very close to the problems which we have just dealt with. We consider here "regulation" (meaning the changed use of the cell material involved) and "regeneration" which rests on the "new production of material." Regeneration is defined as "the real new formation of parts which have been lost" (Dürken). This definition is necessary from the logical standpoint but rather constrains the phenomena since many of the phenomena of regulation can be included as regeneration. For example, if from the ventral surface of a half embryo in the region of the blastopore arises a medullary plate or when the suppressed cell of the first cell-division later forms a half embryo into which nuclear and plasma material have wandered: "post-generation." Regeneration, in the above narrow sense, is far more extensive in the invertebrates; it is not absent in the vertebrates but is limited to the more primitive forms, chiefly amphibia. Again, it is chiefly manifested in certain parts of the body, and in the amphibia only in definite organs. In higher animals and in man it is limited to the capacity for new formation of such tissues as nerve fibres, connective tissue and epithelium in recovery from wounds. It appears, however, as if this limitation is not to be ascribed to a defective potency of regeneration but is the consequence of a limitation imposed by other tissues. Bier was able to bring about extensive regeneration in muscle-tissue when he got rid of these inhibitory influences. The remarkable phenomena chiefly observed in invertebrates, reversal of polarity (in the caudal part the head arises; heteromorphosis: in place of one organ another arises), and the influences which the site of the operation has on the form of the regeneration cannot be described here. They can be got from the literature (Dürken). Here only a few fundamental questions will be raised.

(1) It is to be doubted whether a perfectly typical restoration of a limb, for example, occurs. The typical, that is, created through the constitution of its germ-plasm, individual organization arises in no case. The regeneration arises like the embryonic formation as something new in which the resemblances are more or less lost (within the limits of the normal).

(2) The starting point must be, as can be demonstrated in many cases, a remnant of the old; only occasionally is it shown that the regeneration starts from some tissue foreign to it, for example, a hind extremity, perfectly extirpated in triton, starts from the vertebral column; as has been mentioned, the lens from the iris or from the retina. Moreover, the idea of the "remnant tissue," i.e., the tissue left behind, is to be so understood that this left tissue does not immediately produce the regeneration, but becomes first a young tissue, an indifferent tissue (blastema), from which the further unfolding of the regeneration takes its origin.

(3) The nature of this blastema and its potencies illustrates our theme. It appears in general to be that after loss of a portion of the extremity skin does not arise from skin, or muscle from muscle, or bone from bone, but all proceeds from a newly-formed regeneration blastema. Its cells derived from the adult cells of the cut surface revert to an indifferent condition and are differentiated anew (redifferentiation). So regeneration is founded on redifferentiation or metaplasia. A regeneration blastema would be a significant example of an equipotential system if it actually behaves so (pp. 313-316). The metaplasia arising in the regeneration is conclusive for the potency of the organ-cells.

(4) Such a metaplasia lies at the bottom of those cases in which the germ layer nature does not operate, but originally ectodermal organs are formed anew from entoderm (gut in worms) or the specfic differentiation most favourable for regeneration is found (lens from iris or retina).

Para. 89. Malformations are the result of experiments which nature herself has performed. Many of the experiments described above we meet again in abnormal development. Two cases may be cited. (1) The formation of twins. This happens very frequently in the bony fishes, seldom in the amniotes, yet more seldom in amphibia.

All degrees of twinning are known from fusion only at the head end (duplicitas posterior) or tail (duplicitas anterior) up to the perfect separation into two individuals. Twinning, as already remarked, can be produced experimentally in a variety of ways, through rotation of the frog's egg at the two-celled stage or by the complete or incomplete separation of one of the two cells at this stage. Probably it is this last state in which twin formation probably arises (and in the more perfect separation the single egg twins and doubles). At the same time it is apparent that twinning in mammals and man cannot happen teratogenetically in this period, because in mammals the twins of a single fertilized ovum are characterized by the possession of two amnions and one trophoblast. This would be inexplicable if the separation occurred at the two-cell stage, because then from each of them a trophoblast must arise with a double chorion and a double placenta. It is rather to be believed that in mammals during segmentation some material separates for the formation of the embryo and some for the formation of the trophoblast, and that at this stage the division of the stem cells of the embryo gives rise to twins or multiple embryos.

(2) Phocomyelia is also a good example of the validity of the conclusions derived from experimental embryology. This malformation consists in this, that the anterior extremity is attached to the trunk by a small stump (like a seal flipper). According to its form it may possess the hand skeleton, while the long bones are more or less suppressed. The results of experimental embryology suggest a cause. The skeleton arises through self-differentiating factors, but for their normal unfolding releasing factors are necessary. At what point these releasing factors influence the primordium of the extremity is unknown in phocomyelia. Their effects must also be extremely various, for cases of this condition are known in which the humerus and the bones of the fore-arm are not absent but only much shortened. Since this malformation is heritable there must be present in the germ-plasm an hereditary factor responsible for the differentiation of the limb.

(b) Summary and Criticism.

Para. 90. The foregoing briefly sketched investigations, beside their results which must be studied in the original, and which are in large part contradictory, have brought answers to the questions raised in paras. 84 to 86. The literature on these questions is immense. Let us examine this young science, which is essential for the understanding of how form is derived, and set out briefly the results.

As a beginning we may classify the results into those which arise immediately from the investigation and those which can be inferred from it. The immediate results are three : (1) The primordium of the germ-plasm is not the "simplicity" of the old epigenesists. A high degree of complexity is present right from the beginning in the fertilized egg. (2) This complexity has various fates in the subsequent division of the fertilized egg. It can be divided qualitatively, so that the individual cells will vary in their plasticity, so that later they may not be able to transform themselves into other types. On the other hand, the complexity can be carried beyond the first generation of cells undivided and undiminished, so that these are able to transform themselves and so form a harmonious and undivided equipotential system. This applies not only to the segmentation stages but to the primordia of organs. The converse of this is also proven. The reversal of the limbs from right to left and back again is by no means present in all forms, and in all is only present during a certain time. Only quite a small zone outside the gill region can form gills. The remaining epidermis has not this power. (3) It has been shown that an extraordinarily fine system of dependence of one primordium on another is present; this extends from perfect self-differentiation to the absolute dependence of differentiation processes on other factors.

The more remote conclusions that we may draw from such experiments are two. It is very important for experimental embryology that this inquiry in different forms has brought about results in closely related fields. This was something which this science did not take into its reckoning at first. When one objects that one had "no idea that nature had so many ways out," this objection is valid only for that which has not been levelled against it, but by no means meets the essence of the case that nature did not seek a "way out," but obeyed in each case its inviolable rules which in these cases we did not know. That there is in general a causal sequence in ontogeny—but these relationships have to be worked out in each case, in each group, in each species, in each local variety, nay, in each individual—is an essential limitation which we, in the general appreciation of the results as a whole, must necessarily take into consideration. This limitation is the more serious in that the material available to the experimenter is so small in relation to the enormous extent of the animal kingdom as a whole. Within the vertebrates only fish and the chick have been investigated.

Among the amphibia it is almost exclusively the larval form of our home-bred (German) form which has been the subject of investigation. One might say that experimental embryology is essentially that of the tadpole. This limitation of the material makes any generalization of the results impossible. Apart from all this—and contrary to original expectations—the discovery of such an extensive variation is a great service to this field of investigation. It is, however, necessary to ascertain wherein this variety resides. We shall see that it resides chiefly in the great variety of form, so that a criticism of the results of the experiments is immediately the starting-point of a new morphological inquiry—an excellent example of the real cause of scientific progress [para. 1]. We will now in the next paragraphs consider these new questions.

Para. 91. What does experimental embryology particularly investigate, and how does it investigate it? If every investigation shows us the reaction of the organism to an injury, then this reaction is in a special way influenced by the constitution of the organism. What we then investigate in each inquiry is the constitution of that organism in which we perform the analytical experiment. The answer which we compel the organism to give us is not an answer to a special question, but the only answer it can give according to its constitution. In fact, we do not compel Nature, but it answers us according to the constitution of the disturbed systems.

For a just appreciation of the experiments on living germ-plasm it will be necessary to know how it behaves as a whole in its development. That is, we must know actually, when we wish to understand its constitution, how it appears in all its make-up without exception, and the constancy of its development. The constitution [para. 32] is implied in the germ-plasm. Its influence is apparent in every phase of the development of the germ-plasm, and specifically in every step of the ontogeny. There are three phases in which it first becomes pronounced: cell number, cell size, and cell increase. As we shall see later, the number of the cells out of which the organ may arise is very much greater than we would have supposed. For invertebrate animals precise counts are available. In vertebrates Rabl, firstly, and unfortunately hitherto alone, has investigated the cell number and in one organ, the lens, this has actually been confirmed. On cell size there are yet no extensive investigations. We know that it is a species character. We can compare developmental stages by the cell number and cell size, for example, the gastrula of a sea-urchin, of a snail, of amphioxus, of the frog, might be compared with one another. Cell size and cell number determine the time, rate and continuance of cell increase, for example, the differentiation of the vegetative and animal cells in the frog's egg is clear to the superficial observer [para. 73]. Cell-rich forms must necessarily pass through a longer stage, during which the material produces cell division, whilst cell-poor forms, such as many of the invertebrates which have been used for experiment, quite soon cease dividing and use up their material. The time at which an animal or its organs become adult is subject to great variation. Propagation on the one hand, and the use of what is already complete on the other, are displaced into one another like the dorsal surface of the developing vertebrate embryo.

What we must know is, therefore, always of importance, if we wish to draw rules and laws from the results of our experiments. First, one must have an insight into the homologous relationships of embryonic rudiments—a difficult matter (p. 101). Only with difficulty can the gut rudiment of a sea-urchin and a frog be considered completely homologous in view of the cell number and size. The gastrula of the snail arising from a few cells has in general the same form as the cell-rich gastrula of triton; but what is formed there by one cell is, in this, the result of many (Rabl). The lips of the blastopore of an amphioxus larva or a petromyzon larva in which the ventral surface produces ectoderm, neglecting the form, cannot be directly compared with the same areas of the frog larva in respect of the destination of the cells. How these things behave later in the germ layers we do not know.

The significance of the zones of proliferation (these lie alongside of and within one another owing to increasing indifference, and also to the differentiation that at once arises from their functions) necessitates a microphotographic knowledge of the developing and the established primordia which we do not yet possess, but which we must know precisely when we introduce a glass needle into the germ-plasm (just as the topography of the body must be known in a surgical operation). As soon as one makes this topography the object of the experiment—and this one can do—one uses the experiment in a truly causal way, i.e., in order to get an analytical insight into the constitution of the germ-plasm.

It is in this direction that Braus has been conducting his research by which he intended to test the invisible differentiation of the mesenchyme cells, and has established the fact that cells have already become defined as future cartilage formers as early as the mesenchyme stage [cf. para. 29].

From what has been said there arise now the important consequences, that the determination of the cells (formation of the primordia) and the later differentiation (formation of the different cell-complexes) must arise discordantly. This discordance in the development of the germ is not the same, for example, in the frog, turtle and triton. Within the same ontogeny the determination, the differentiation, the limitation of potency [para. 86], and regulation of factors may be expressed very differently in different parts of the germ-plasm. This is actually so. The differentiation of the axial organs, where earlier the formation of the head took place (this has long been known), starting from the front towards the posterior (p. 267-8), is a witness of the displacement of these things. Lately the fortunate term "mode of differentiation" has been introduced (v. Ubisch). The differences of gradient may actually explain how the same experiment in the larvæ of different species of urodeles must have different results (Brandt) because the determination of the indifferents in them is caused to proceed at different rates, and so the result differs markedly.

At some time for each cell-complex the stage of final primordia must be reached, that is, the state of the cells in which they have begun their determination for the later differentiations. If we believe that this goes hand-in-hand with a limitation of the determination and the potency, then the question arises in what manner and way do the potencies become expressed in the cell? It would seem as if at a definite time in the cell there are aroused capacities with all their later implications in normal behaviour, but as yet only for the unfolding of definite organs and systems. Thus we have what we can call a cell tree, a cell race (cell lineage).

Normal development has shown with certainty that there is such a cell lineage. In the invertebrates it can be followed pretty generally from the egg (Korschelt and Heider). It displays itself quite early during the segmentation of the egg, which provides the ectoderm, entoderm and mesenchyme. They become at this early time primordia, so that if they are destroyed definite defects follow. In the vertebrates cell lineage up to now has not been demonstrated; it is not even suggested, since the immediate purpose of cell division is the provision of cell material (Peter). A large cell territory here corresponds to the single cell of the previous example (Rabl). More strikingly the mammalian egg resembles the invertebrate in the production of segmenting cells externally distinguishable from one another. There is at the moment no certain proof of cell lineage in the vertebrate egg. In the study of histogenesis some observations have been made which compel the adoption of such a conception that cell lineage must also hold in the vertebrate. This applies firstly to the germ-cells which we, with as high a degree of certainty as is the case in the invertebrate, derive from no germ layer but from the fertilized egg itself (Lubosch). Further, we know that there are many organs (hair, sense organs, taste buds, glands, intestinal villi, lungs), whose primordia increase themselves *in toto* by budding (M. Heidenhain). Followed backwards this leads to a very simple primordium of the gland or the lung, i.e., from a single ancestral epithelial cell (Heidenhain, Bender), and this further back to a few, and in one case (thyroid) to a single ancestral gland cell (Heidenhain). If one can refer back all the taste buds, all the hair primordia, to a single ancestral hair-cell, is at present not known. That the hair primordia appear diffuse is no objection to this, for in the earliest stages of development a few or only one cell is sufficient, as is actually the case for many organs of the invertebrate. The early establishment of the serial position of the hair rudiment suggests at all events that such a series arises through the division of one primordium (Maurer, Ludwig, Robertson). These observations that have been made on vertebrates make it necessary to accept the idea of cell lineage. Somewhere in the cell-rich organism there must be found a separation of the ways that lead to the establishment of its many organ-formers.

If finally there is a specially differentiated starting point for all organs the same should hold for whole systems, e.g., the gut. This question, however, is difficult to answer. A third question thrusts itself forwards. The formation of mucous membrane characteristic of small intestine in the large gut which, as above mentioned, has recently been observed in the adult man, suggests strongly that a final distribution of the rudiment has not been achieved. This explanation is, however, hasty if a perfect histological explanation can be found. It is an example of the necessity of avoiding hasty conclusions. For a long time a tunicate, clavelina, was regarded as as example of regulation in the sense of a harmonic equipotential system. This animal appears to have a wonderful capacity for forming typical organs out of any living fragment, and according to the size of the fragment a reduced representation of the original. It has, however, been shown (Schaxel) that these new formations do not start from remnants with a behaviour planned with wonderful foresight as has been taught; these without exception die. But cells which, during the differentiation of the body, had persisted in an indifferent embryonic state provide the regeneration which behaves according to the type of embryonic new formation. A similar case may therefore arise in the unfolding of the gut mucous membrane.

Similar criticism may be applied to those regeneration systems which have been described as harmonic equipotential systems.

If experimental embryology is inclined to look on cell division as something heritable there is neither the compulsion nor the need for such an idea.

What urges this is particularly the phenomenon that differentiated cells can undergo dedifferentiation (glands, epithelium of sense organs, endothelial cells, cells of reticular tissue and many others). This has been called metaplasia [para 95].

Quite generally we believe that such cells are not perfectly determined, but that only a part of their capacity is activated while the rest remains latent.

Weismann, the creator of the science of dissimilar inheritance, had formed the conception of a reserve of idioplasm. This conception is too vague to be taken literally; at least, as a picture it is satisfactory, since it only involves the acceptance of cellular regeneration activated by the germ-plasm.

We must think of the relationship which holds between the cells chiefly as something dynamic, whilst hitherto we have spoken only of the material constitution of the germ. It has been shown that cells which have been cultivated outside the body are incapable of normal tissue formation. They grow, divide unequally, without showing any differentiation, and are of course the same cells which inside the body form tissues and organs. This compels one to believe that it is the dependence of cells on one another that leads to differentiation. This is also of influence on the question of the greater or less limitation of potency. The normal behaviour of ontogeny depends on those unknown laws that govern the germ-plasm. But differentiation in itself is considered not only as a formative process, not a destiny which hangs over the cells, but a vital function of the cell (Weidenreich). Every cell division is a function of the cell. Cell division and differentiation have been correctly linked together. The number of cells, to which we refer in more detail later, is of significance [para. 105]. Only cells capable of division can naturally undergo further differentiation. The supporting cells of many epithelial structures are not yet fully differentiated cells (matrix cells), whilst only few cell groups, which are already fully differentiated, have the capacity of dividing and differentiating (gut epithelium, gland cells, cells of connective tissue formation). The process of cell division itself appears to be that which brings about a rejuvenation of the cell, that which gives the possibility of unfolding in another direction; cell division can be looked on as the whole developmental capacity of the cell which can be brought about in the cell by purely dynamic factors without the necessity of a reserve of idioplasm (Weidenreich).

All these (the homologies of the primordia, their microphotography, the various differentiations, the temporal and spatial relationship of determinants to indeterminants, the extent of the preservation of indifferent cells and the part of dynamic factors in cell differentiation) we must know if we wish to deduce from the results of the experiments a science of the ætiology of development. Indeed, we must know more; especially the nature of destruction which we achieve by the experiment. Then if all the factors are the same and not interchangeable, the inquiry will only then discover a new factor which was not there before. One observes also that the capacity of an organ or an organism to react to the stimulus is considerable but not unlimited. Ear cartilage cannot react to a pull, but rib cartilage does. Animals, in different degrees, take no carbon particles into their lungs, whereas the human respiratory passages cannot escape them. One cannot, therefore, investigate the processes in the development of anthracosis in mammals in a cartilage outside the affected area without obtaining doubtful results. There is here a norm for the reaction possibilities. Experiments take for granted that the organism can respond [para. 44]. Mosaic eggs are not suitable for the study of regulation. Regulation eggs are suitable for the decision of questions of localization. The responsibility and irresponsibility of the germ-spasm militate against the inquiries. Their effects we do not know, but it is necessary that they should be determined. Questions and discriminations are therefore possible here before the causes of the formative processes have been obtained experimentally.

Para. 92. Experimental investigation has given us insight repeatedly into the conditions under which an animal acquires its form. On the whole, these have been confined to one type only, external and internal views of an abnormal state of affairs. In the beginning of cell investigation, as Henle expressed it, each new layer placed under the microscope was heralded as a scientific discovery; experimental embryology is in this state at the present time. Each fresh experiment is hailed as a new discovery. When the science of cytology was developing it was only slightly less modest. There is yet no science of the conditions and causes of development. We do not know if there will be or even if there possibly can be. The "specific form that life develops" includes these two ideas. How does it become expressed (historical, causal) and how does the expression arise in the organism (onotgeny, conditional)? Since the form is alive, development is a vital process of the germ. Its essence resides in the unity of the processes which we can appreciate only as isolated elements. To us these processes appear as a conglomeration, therefore chaotic; in the germ they are an ordered whole. We cannot comprehend the factor of life. This is the justification of all our earlier discussion [para. 13]. When the limits drawn there are known, whether appreciated or not, there are two ways in which the investigation may proceed; either to investigate within these limits the mechanism of development, or to obscure with meaningless scientific terms what simply lies outside the scope of scientific investigation. Roux has followed the first path which is in accordance with Kant's limits of scientific knowledge (p. 7). He does not insist on the ætiological aspect, as is often believed, but turns much more to the architectonic characters of ontogeny, which also involves the mechanism of development. Unfortunately this purpose, which promises clear results, is pushed into the background by blind experimenters, so that we are embarrassed in appreciating the results of these experiments which lack all morphological foundation. We cannot say and we cannot investigate what "the form" of the gills may be but we can consider the formal relations of the gills scientifically and determine instead through analytical experiments the partial cause. How the form of the gills and the partial cause co-operate in the development of form we can only apprehend by some understanding of the series of ordered events which may be shown to exist here [para. 24].

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(C) The Succession of Events in Ontogeny.

Para. 93. Experimental embryology in a more critical appreciation of all the facts has produced this result, that in the investigation of the "what" and the "why" of development the "how," which is the kernel of ontogeny, has practically never been considered (Vogt). In a more emphatic fashion it is shown that all the knowledge of the formal and the dynamic processes, even if they were creative, does not tell us how the cells of the germ begin to form a gastrula or a dorsal ridge or a notochord. We only see that it happens. We observe a movement, a change of form, a transposition and an accumulation of cells whose end-result is the formation of the embryo. The conception that the whole germ exhibits a form of amœboid movement, within which the individual cells are shaped, appears to the author (Vogt) as the only thing of any use in trying to understand the whole affair, and surely this is so.

In this discussion it has not been sufficiently emphasized that morphology has long recognized this as the fundamental problem, and it has explained that the entogeny may be inconceivable in itself without reference to the phylogeny. Then this, which, in a wide sense, can be regarded as an amœboid movement of the whole germ-plasm, is only the ancestral repetition of processes which are historically bound up in the germ but are liberated in fertilization and then unfold themselves (palingenesis). Naturally this explains no more than the other attempts, for we have no idea how these changes arise in the germ [para. 31]. But this explanation has obviously this advantage, that it does not postulate as sufficient an "ontogeny in itself," and cannot. This we must now shortly explain.

It is a fact that in every ontogeny there occur, as a temporary condition, states which in earlier forms reached a final and persistent form. This admixture of ancestral and germinal development shows how the individual ontogeny is affected.

This ancestral development plays a part in the development of the whole of our bodies. The organs are developed before they receive the stimulus of function (first non-functional period of development (p. 41), eye before light is perceived, brain before there are conducting paths, joints before there are movements). Precisely in these facts occurs the parallelism mentioned above. The stages traversed in the development of the human heart are perfectly similar to the adult stages of the heart in the urodele amphibians (Benninghof.) The ear possesses temporarily a ductus endolymphaticus which opens freely to the exterior. This state persists in fishes and many others.

From this point of view one has to estimate the appearance of the gastrula in every ontogeny. Of course the temporary embryonic stages are related to the persistent adult stages (the fertilized egg to the protista stage, the blastula to the cell colony, e.g., sponges). There are many things here to think about [para. 104]. The gastrula, enclosed only by one of the two cell-layers, and with a stomach opening to the exterior (gastrea) is correctly related to its mode of life. It has now acquired the status of cœlenterate. Haeckel's gastrea theory taught that in the beginning of organic life the gastrea (embryo with a stomach) formed at one time the highest organization.

There are a few metazoa which persist at this stage. Others have advanced from this stage in various directions. The gastrea stage may, therefore, arise in the ontogeny of every organism.

Many attempts have been made to explain gastrulation on mechanical principles.

We may refer to two of these. Firstly, the limitation of space to which the macromeres are subjected by the micromeres; these micromeres grow from the animal pole downwards towards the less actively dividing macromeres; secondly, the macromeres, owing to the narrowness of the space, take on a form in which they become keel-shaped towards the segmentation cavity, which is here broader. According to well-substantiated experiments (Bütschli, Speck) this becomes so extensive as to cause the transformation of the blastula into the gastrula. One can therefore well believe that the gastrula may be only the basal form of all metazoic development, since it must of necessity arise from the great variation in size of the segmenting cells. The variation in size may be again only the consequence of the polar differentiation of the egg arising from the presence of the yolk [para. 74].

It must be admitted that every living process must obey mechanical laws. An insight into these laws does not, however, furnish a full explanation of the origin of the processes themselves. It is very instructive, as has been demonstrated, that the vegetative cells of a triton gastrula pass through a change of form as if forming a gastrula, even if one takes away the animal pole. There is nothing present then which can exert the "pressure" necessary in the above explanation (Vogt.) Gastrulation rests on a self-differentiation of the cells. It explains also why the primitive development of all vertebrates must pass through, as an inevitable necessity, the gastrulation process, the invagination of the chorda canal, the formation of the neurenteric canal, etc.

If gastrulation is an ancestral process then at some time there must be a gastrea existing as an independent animal. Naturally no such animal is known. Yet it has often been figured.

The nearest to it is that of a swimming ciliated globule, which one might regard as a primitive metazoan. In this there arises, through the persistence of movement in a definite direction, a differentiation into an anterior and posterior end. The posterior end withdrawn from the resistance of the water has taken on a nutritive function, and for the better exercise of this function has sunk more and more into the interior of the animal (further cf. in Korschelt and Heider, cf. literature, p. 291).

Examining this parallelism which arises between ancestral and germinal development, the idea comes as if each step, which looks like an advance in the ancestral development (that is, in the speech of the geneticist, every newly arising ancestral feature) prolongs the germinal development of the subsequent events about one stage. Haeckel has described this as the biogenetic law ; O. Hertwig as the ontogenetic causal law. The assumption here is that these new structural formations in the germ-plasm are laid down at the same time as the youngest of the micellar structures present, that all are laid down in a historical sequence, and are released ontogenetically in a definite order in time.

We now know, however, of types of localizations, which in themselves have nothing at all to do with hypothetical ancestral factors, and also nothing if a definite spatial localization of the primordia [para. 120] is possible. They proceed to their unfolding in a definite temporal order. It looks as if we wished to avoid deliberately the implication of the term "law."

We speak enthusiastically of the ontogenetic recapitulation law (Roux). Roux explained the relation between the structural changes in the germ-plasm of the ancestor and its time of unfolding subsequently in development, by the idea that only such changes have been retained which allowed the fundamental form of the germ-plasm to remain unchanged, otherwise every new ontogeny would have to arrange a new basis, for it would be disturbed by the effects of every change.

We may here consider the relationship between this explanation and that based on the hypothesis of ordered events [cf. also para. 120]. This parallelism between the ancestral history and the germinal history does not always occur without modification (palingenesis). Often differences arise which principally rest on this, that there always appears, beside the typical formation, a structure conditioned by the development of the primordium. These primordia are, however, specific, and have a regular distribution (yolk) in any one egg, and are governed by specific conditions in the development (e.g., the intrauterine development in mammals). Thus the ontogenetic recapitulation is changed most specifically (cænogenesis, from the Greek kainos—new).

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Veit. See p. 293.

Vogt. See p. 293.

(III) Morphology of the Tissues.

Para. 94. If the morphogenesis of man provides answers to promorphological considerations [para. 72] it also provides more important questions of structural form in the production of the cell material. This material does not persist unregulated, but, on the contrary, is subject from the beginning to ordered influences upon which the formation of the body proceeds. We would remark that the transformations of cells into organs proceeds along the path of the tissue connections, and a series of important questions is based on the nature of these connections. These we must straightway concern ourselves with. The questions thus raised necessitate discussing the morphology of the cell in some detail.

(1) The Conception of "Tissue."

By a tissue one understands the association of similarly differentiated cells according to a definite principle. Here is raised at once the question: Is such a conception valid? If there is a science of the tissues there must be a tissue on which it is founded. The above definition is based, however, as is easily perceived, only on the ideas of the principle of association and the degree of differentiation. Both we first abstract from the form and structure of organs. Therefore we are saying at once, that what we call the "texture" of a tissue derives its meaning from the "principle of association of like elementary parts." In no case is there such a thing as an isolated tissue which can be contemplated purely objectively and distinguished as something of a similar or subordinate order to the organs. One surveys the objects of histological investigation. Such are always bits and fragments of organs brought under the microscope; never, however, a tissue.

In the body there are really only cells and organs, while tissues as such do not appear except only to represent the principle according to which similarly differentiated cell complexes fuse together. This erroneous idea that between cells and organs there exists a third element called tissue, is based on and determined by our method of teaching that passes from cells to tissues and from these to organs without making it clear these three things represent terms of quite different values. The scientific terminology of the finer structure of organs has always been very sharp and exact, and its progress has given rise to several subdivisions. The science of the structure of cells is called cytology, while that of organs is called microscopic anatomy. To the organs we ascribe an outer form and an inner structure composed of different elements. The science of tissues is called histology; it investigates the texture of similarly differentiated elements. There are accordingly in an organ three different things to investigate. (1) The form of the cells. The comparison of the form of all cell types of all organs is the purpose of cytology. (2) The different rules according to which similarly differentiated cells are bound together (texture), so that within the wall of the gut we should note the texture of the cells at the epithelial border, the muscle cells in the muscularis mucosa, the fibres in the mucosa proper, and submucosa wherein there would be distinguished fibres predominantly connective or predominantly elastic. One can extend the conception still further as soon as one recognizes that the texture of the muscle cells is the same as in the wall of the blood-vessels and the bronchus, etc. In this way, and only this way, one arrives at the conception of a tissue of smooth muscle, something which is more than the organs in which it exists.

Modern histology has followed the example of the older "general anatomy," which, as earlier shown [para. 12], collected the same elements in the organs into a new entity. This explains the term general anatomy applied to this form of anatomy, the most specialized science of all (Gegenbaur). The term can only be understood from its history, and since it is likely to lead to confusion it would be best to drop it.

Only when the texture of the different groups of variously differentiated cells forming an organ is known, we can advance to the third part and proceed to the investigation of individual organs, that collection of different elements in a single mass.

When we come to study these we speak of them as individual objects, our purpose being to analyse the anatomy of the organ. This, however, does not bear witness to the higher value and fundamental significance of the notion of tissue. On the contrary, it teaches us to treasure very highly its importance, as the following will make clear.

Probably there are similar considerations which, without having arrived at a full insight into these relations, will now wipe out the boundary between histology and microscopic anatomy entirely, in which a special presentation of the study of tissues will be avoided, and the individual tissue will be described as part of the organ. The bony tissue, however, is not the "bone," the muscle tissue not the "muscle," the nervous tissue neither the central organ nor the peripheral nerves, though the principal part of this organ will be formed by it.

The deeper understanding of the relations of tissues and organs to one another is hindered by such ideas as these. The essence of the study of tissues is based on analysis and systematization. The analysis of the organ separates the dissimilar from one another; first, intellectually, then as far as is technically possible, also mechanically isolating, at the worst optically isolating. The systematization groups the like of various organs into an intellectual whole which now arises as a pure abstraction in the conception of tissue.

The study of tissues bears the same relation to microscopic anatomy as does grammar to speech, or logic to thinking; a presentation that knows no study of tissues would be like a study of language without grammar. Instead of a scientific study of a language it is often thus pursued, with the result that the use of the language may be acquired, but no understanding of it is obtained. This might be satisfactory for the purpose of instruction; for the appreciation of anatomy as a science, the dangers of this path cannot be too emphatically presented to the beginner.

That the essence of the relations between histology and the microscopic anatomy is misunderstood, is shown by the term "general histology." This is, perhaps, only a hybrid, indicating without any deep reflection a connection between the old "general anatomy" and the "histology" of the present. If it be something else then it ought to be a "special histology." This might do, but it would only be again microscopic anatomy, which, however, is false, since the organs show only a formation from tissues. The dissimilarity of their parts constitutes their essence in contradistinction to the tissues which possess similar elementary parts.

(2) Specificity and Classification of the Tissues.

Para. 95.—A good classification of the tissues, said Kölliker in 1889, is a difficult task. This difficulty still persists, and the longer it persists the worse it gets. The difficulty lies in this, that no principle of classification, choose which we will, is in itself valid and free from objection. A classification according to form and position is the most fruitful, but is not exhaustive since it must ignore derivation and origin. A classification according to function is the most useless; it tears the whole into too many parts, and must, if it would be distinguished from a mere enumeration, at some point classify functional dissimilarities in some formal way. A genetic classification (according to the germ layers) would be best, but it is the most difficult.

A good classification is not only a difficult task but also a very necessary one, particularly with reference to the needs of pathology. With the question of the classification of the tissues goes the question of their specificity. This again may be functional or genetic, "physiological specificity," that is, how far a tissue can reproduce only the the same (homoplasia), or another tissue (metaplasia)—"genetic specificity" if a special mother substance (germ layer) can form only the same or different parts (specificity of the germ layers). In an appreciation of the value of the different classifications we will start from genetic classification because it includes the most fruitful problems, and the most is to be got out of it.

The specificity of the germ layers was never maintained more firmly than now, yet there are differences of opinion about it. One only denies the strong specificity because there are too many exceptions; others, on the contrary, positively ascribe to all the germ layers the production of all types of tissue (all may produce all, cf. p. 301). A third opinion (Voit) denies, of course, the histogenetic specificity of the germ layer, but maintains that their organ specificity is proven.

In the appreciation of the task before us we must keep in mind that we have only to do with healthy, uninjured tissues, though the second of the recognized groupings excludes this. We are not concerned with what happens when a cell is destroyed, but what it actually does in its undisturbed behaviour, not with its potencies, but with what it now is [para. 80]. Further, there is, unfortunately usually overlooked, a more important difference, first brought out by Rauber, between the conception of a "tissue" and the investigation of a specially defined tissue connection.

Epithelium in itself is a conception which is subdivided into numberless individual specific epithelial types. If we thus group the tissues in our mind naturally the reason cannot come from any specificity of the germ layers. Only cells, not ideas, have specificity. This logical failure makes it easy to deny any specificity [para. 28]. Then every germ layer can form epithelium. Cartilage and muscle tissue can come from mesenchyme as well as from ectoderm. Cartilage and bone tissue can arise from various matrices. If one, however, does not adhere to a conception so minutely divided, but limits it as narrowly as possible, then the statement is reduced considerably in favour of specificity. Then the epidermis, sense epithelium, sebaceous glands, are derived only from ectoderm, mucous-secreting or absorbing epithelium from entoderm. Consequently one does not arrive here at a perfect specificity because, in the organization of forms widely different from one another, there will still arise morphological and functional similarities of the various germ layers. For example, mucous-secreting epithelium arises from ectoderm in the fish, horny epithelium from the fore-gut, and therefore from the entoderm.

We are therefore compelled to give up the histogenetic specificity of the germ layers. It would be more successful to adhere to an organ-forming specificity of the germ layers (Voit), like the long-recognized conception of Remak, whereby nervous systems, epidermis, and sense epithelium are formed only from ectoderm; gut epithelium only from entoderm; striped muscle only from mesoderm; blood-vessels, blood, skeletal organs only from mesenchyme. Obviously there are exceptions. The epithelium of the bladder is derived in one organism from mesoderm, in another from entoderm, in a third from both. The reference of the chorda to a definite germ-layer is not established in view of its development in the different vertebrates (Veit). The vascular system arises from entoderm or mesoderm. In these cases we must describe these organs as dissimilar from one another (not homologous). Perhaps we are not right in so doing. It may be referable to differences in the original layers. The cells forming the organs in any individual case of development may start in different germ layers (pp. 313-14).

The specificity of the tissues and the germ layers plays a part in all those processes in which there is present renewal, compensation, and new formation of tissue. Renewal by tissue is found physiologically in all organs whose cell number is not normal (matrix cells of layered epithelium, compensation by bone cells and dividing tissue cells, gut epithelium, gland cells, cells of reticular tissue, stem cells of red and white blood-corpuscles). The regeneration processes, reviewed earlier, belong here. Under new formation are included especially the products of chronic inflammation (tubercle, gumma and the tumours). In the appreciation of all these processes the point is, do the newly-arising tissues come from the same elements or not (homoplasia, metaplasia)? For the tissues as a whole homoplasia appears to be the rule. Epidermis regenerates itself only from epidermis, connective tissue only from connective tissue, vessel from vessel, nerve-fibre from nerve-fibre. But soon in individual case metaplasia arises, when the typical cell form and cell variety can be compensated. Goblet cells do not arise from goblet cells but from columnar epithelium. The regenerating nerve-fibre arises from other cells (such as the cells of the sheath of Schwann) than those of their embryonic origin. Metaplasia in the exact scientific sense is present when one tissue changes into another. Normally and pathologically this process is limited in that one accepts the existence of the metaplastic process in the two vegetative tissues (epithelium and supporting tissues). The chief examples are the formation of connective tissue from endothelium (horny skin), of endothelium from connective tissue (the formation of new capillaries), of blood-cells from connective tissue or endothelial cells, the different blood-cells from one or more mother cells, formation of bone from connective tissue, or cartilage from connective tissue. There are numerous problems and they are very differently answered. So much one can say, that metaplastic compensation certainly occurs. The extent to which it occurs will depend on the view that is taken of the state of differentiation of the matrix cells. So long as we, for example, hold that all mesenchyme cells, in the absence of all morphological differences, are the same, the ubiquitous derivation of cartilage from connective tissue is to be regarded as the metaplasia of one supporting substance into another, though, strictly speaking, the homoplastic formation (cartilage from cartilage, bone from bone) cannot be excluded, since the proof of the non-specific nature of all mesenchyme cells is not provided and at the moment cannot be settled (p. 297).

In general, therefore, metaplasia is limited to a narrow field. Further, that the process holds right to the limits of the germ layers is strongly disputed. The question of specific mother cells is very important in the case of tumours, in which descent from the germ layers becomes a principle of classification (epithelial tumours, connective tissue tumours, etc.).

With this understanding that we are not clear on the homology of the germ layers in respect to their cell content, we come in contact with deeper problems of great difficulty which this question of specificity raises. We can in general rest on the earlier statements [paras. 90-92] and commit ourselves to the following only. The conception of germ-layers arises with the beginning of modern embryological investigation. Plants and animals will be constructed from the "germ-layers," these being regarded as the ancestral organs. Thus the conception has developed that the germ layers are preeminent in the hierarchy of the divisions of the body, that they stand as a special entity between the segmenting cells and the organs. On the basis of the study of gastrulation, particularly the formation of the chorda, the problem has been explained in this way, that the chorda cannot genetically be brought within the germ layers (O. Hertwig, Veit), since this arises partly from the entoderm, partly from the dorsal lip of the blastopore. So one arrives at the more correct idea that in the germ-layer formation it belongs to the order of material already specific for the primitive organs. These are not subordinated to the later organs, but as primitive organs are included with the later organs.

The description of a germ layer as entoderm, i.e., purely topographically, ought to have no influence; at the same time the entoderm is also an organ, namely, the primitive gut which in its walls contains the rudiments of other organs.

The further problems are these :—

(1) Is there a special cell stem for each organ which in the last resort can be referred back to a special group of multiplying cells?

(2) Is this cell found at equivalent stages of development in different animals always at the same stage of differentiation?

(3) In the different animals can this group of cells always be derived from the same germ layer? Before these questions can be properly answered the question of the specificity of the germ layer should be settled.

These three questions have been dealt with above [para. 90].

The first question can be answered affirmatively with a high degree of probability. The second question is to be denied, since the degree of differentiation depends on the number of cells and the rate of division. The third question is also probably to be answered negatively. In the case of the mesenchyme, however, the evidence may be considered especially complete. This tissue admittedly proceeds principally from the mesoderm, inasmuch as cells separate from their epithelial connections and form branched elements, out of which later connective tissue, tendon, cartilage, bone, vessels, blood- and lymph-cells, chromatophores and fat-cells arise. It is in itself unreasonable to accept that the many valencies which give rise to these different formations can arise only through external influences. This is just as improbable as that different beings could arise from the same egg-cell. It only appears to be so because all these elements at every stage of embryonic development appear to be the same under the microscope. Here we ought experimentally to be able to show what these cells can do, since we are not able to show morphologically what are the essential differences in the cell stem.

The mesoderm, the essential source of the mesenchyme, derives its elements from many sources, from the dorsal lip of the blastopore, from the region of the primitive streak, from the dorsal and ventral region of the entoderm. It appears certain that in different animals the material which at one time is carried to the mesoderm is at another time retained in the entoderm (e.g., cells forming blood and vessels). In some cases then the entoderm would be endowed with the capacity of forming blood-cells, whilst at another time this capacity resides only in the mesoderm. The cartilage-forming cells are obviously widely distributed throughout the body and are inconspicuous, since everywhere cartilage can arise in a series of definite stages, or it arises normally in many animals, whilst it fails in homologous animals in the same organ (heart, sclera of the bulbus oculi). One ought, therefore, to conclude that every mesenchyme cell possesses the extraordinary specific capacity to form chondroitin sulphuric acid whenever pressure or weight or some mechanical stimulus affects it. It would be more appropriate to prove that mesenchyme possesses these cartilage-forming valencies. In the majority of cases one can prove that definite mesenchyme cells distinguishable from their neighbours by no external feature would be advancing toward cartilage formation.

If some animals possess cartilage in the interventricular septum, others in the outer tunic of the eye, it might well be possible that at homologous points in other animals there are present cells which could produce cartilage only by special stimulation. The perichondrium is well in the position to accumulate mesenchyme cells which later are transformed into periosteum, but which can become the starting point of cartilage formation in callus. Cartilage-forming cells used not to be foreign to the cranial bones, arising now from connective tissue, when we remember that in primitive forms the brain is covered by a cartilaginous primordial cranium. The long interval of phylogenetic development does not invalidate an inheritance of embryonic topographical relations which are not used at all to produce phænotypical results. We may briefly allude to the possibility that the cartilaginous nucleus, so long described as secondary in the condyle of the lower jaw and on the articular surface of the temporal bone, is derived from the primordial cartilage (Lubosch) of bony fishes. Also the capacity of the synovial membrane to form cartilage is on the ground of comparative anatomy to be referred to the ancient possession of cartilage cells (Ders).

The same applies to the scleroblast. In view of the special organization of these remarkable cells there can be no doubt that the osteoblasts are only mesenchyme cells which can be stimulated to bone formation in places of activity. It has been asserted that these cells are of ectodermal origin, and have become secondarily embedded in the mesoderm. All investigations directed to confirming this origin have up till now been negative (Scily). On the other hand, though their specificity has not been confirmed, the supposition has not been disproved that they might reach their functional activity by descent through a specific cell line. Specially we should bear in mind the vessel wall in whose vicinity the osteoblasts prefer to arise. With the most recent methods there is nothing to be discerned about the development of these cells. Suddenly they are there; the mesenchyme cells form nucleus and plasma at a definite moment so strikingly that one has the osteoblasts in front of him in an instant.

The same applies to the fat cells. Not every mesenchyme cell is a fat cell. Not every mesenchyme cell can become a fat cell. If a fat cell loses its fat it does not become a connective tissue cell, but a defatted serous cell.

Fat cells differ very much from each other; many start originally in the cell stems which give origin to the cartilage-forming series. This origin is confirmed by the fact that certain cartilaginous skeletal parts can be replaced by masses of fat, as, e.g., the epiglottis or the fat columns (Lyssa) in the tongue of mammals or parts of the cartilaginous joint capsule as it arises in amphibia through fat cushions (e.g., in birds, Lubosch).

These remarks are not to be taken as "proofs," but as hints that the ubiquity and the defect of any specificity in the mesenchyme are not so straightforward as to need no further proof. There is a further consideration. The mesenchyme is by no means of pure mesodermal origin only. That this is so has been realized ever since the discovery that the mesenchyme cells grow into the empty spaces between the germ layers. Between the germ layers a plasmatic continuity in the form of plasmodesma is present before the arrival of the mesoderm (cytodesma, Studnitzka, epithelial connective tissue, cf. Held). The mesenchyme cells penetrate this plasmodesma and usurp the paths formed by these earlier connections (Held). This material arises not only from mesoderm but also from ectodermal elements (Held, Veit). It may be that these primary connections, which are part of an active and specifically effective plasma of cells, exert chemical influences on the in-wandering cells, or such may be exerted by the in-wandering cells (cf. chiefly Held, p. 21 ff).

The development of a specificity at different moments can thus be explained, and the specific result may be the compromise of many factors. Anyhow, in the investigation of this question of specificity we are right at the very beginning, and all dogmatic opinions for and against are at the moment to be avoided. Only probability can point in one or the other direction, and nothing that has been said excludes the possibility of specificity.

Para. 96. For all these reasons it is most advantageous to adopt in classification a formal principle and to keep the formality in the foreground. In respect to the so-called animal tissues we cannot ignore their functions. We have therefore the following groups:—

(1) The epithelial tissues. This is a tissue which arises only from cells and their connections (cyto-plasmodesma) and covers surfaces (genetically from all three germ layers and the mesenchyme endothelium).

(2) The supporting tissues. This forms a deeper tissue and arises from cells, ground substance, and intercellular fibres (genetically from mesenchyme preferably, but also from plasmodesma [epithelial connective tissue] of all germ layers).

(3) The muscle tissues. This arises only from cells (smooth muscle cells, heart muscle), or from cells fused into fibres (striped muscle fibres) whose special functional element is the contractile fibril, genetically from mesoderm (striped muscle), ectoderm (smooth muscle in part), mesenchyme (chief mass of smooth muscle and heart muscle).

(4) The nervous tissues. This arises only from cells and their processes in the service of nervous conduction. In addition it forms the investment of the nerves (genetically it arises only from ectoderm).

(5) Cells without tissue connections. Cells of the blood, the motile cells inside and outside the vascular system (plasma cells of

the connective tissue). The sexual cells must also be included in this group.

If one wishes to carry out a classification of the tissues according to a functional principle, then there must be distinguished as superordinal groups, germinal and somatic tissues (Rauber, Weissman), of which the first includes the sexual cells, perhaps with inclusion of the tissues standing in the immediate service of their development and nutrition (interstitial cells, cells of Sertoli, follicular cells). The latter, the rest of the body tissues which can be grouped according to their specific properties.

This classification is bad since the functions of cells fall into innumerable subgroups. It works best in the consideration of the individual tissues.

No classification is perfect. The one described has its defects. The chorda tissue may be described as a supporting tissue. It is put down mostly in the supporting tissues, but can be quite correctly included in the epithelial tissues (p. 335). The neuroglia, since it possesses no nervous functions, can be separated from its intimate connection with the nervous tissue and placed under the epithelial. The whole mass of neuroglia is to be regarded as an epithelial sheet whose elements only retain their epithelial connections at the surface (ependyma), whilst in the depths, on the contrary, it forms branching cells with intracellular fibrils differing widely from one another (Held). In respect of the muscular and nervous tissues, Stohr, senior, has observed that there can be no reason for regarding these as tissues in the strict sense, since they are mixed so intimately with other tissues in consequence of the predominance of elements differentiated as muscle fibres, nerve cells, and nerve fibres.

This is to be rejected in the case of muscle tissue. The sarcolemma belongs to the muscle fibre, therefore to muscle tissue; the internal perimysium that envelops each muscle fibre belongs to the muscle fibre as little as does the loose connective tissue that holds the fibres of the tendon together to tendon tissue, or the Sharpey fibres to bony tissue. This substance belongs rather to the muscle, to the tendon, or to the bone as organs. In regard to the nervous tissue the views of Stohr would hold so long as the nature of the sheath of Schwann and its nuclei remain obscure. Only if they, as Schultz believed, actually are related to the axis cylinder as the sarcolemma and the nuclei are to the muscle fibre, only then would the conception of a nervous tissue be valid. If however, the cells of Schwann and the neurilemma have other origins (neuroglial elements [Held] or mesenchyme cells), then pure nervous tissue would only be found in the central nervous system.

(3) The Promorphology of the Tissues.

Para. 97.—The differentiation of the tissue cells (the establishment of structural differences) is apparent in the interior of the cells, on their surface, and in their form as a whole. In the interior of the cells there arise as differentiation products granular and thread formations, vacuoles, fibrillæ, many inclusions and cell products (secretions and pigments, etc.). The cytoplasm of the cell-body shows different densities (known as cortical plasma, exoplasm and endoplasm). The surface of the cells may be covered by an investment (cilia, flagella, cuticular border); the latter may be the site of absorption in a specific direction (porous canals). These differentiations, whose individual description does not concern us, do not arise irregularly, but permit us to recognize a definite spatial arrangement and show themselves subject to a law of "extraordinary simplicity and range" (K. Rabl). It is the law of the polarity of the tissue cells. Probably the fertilized egg is already differentiated polarly (p. 163). All egg cells with large masses of yolk are certainly polarly differentiated. Cell colonies, as volvox, exhibit always a polar differentiation into a free and a basal surface in the cell membrane of the cells. In the metazoa the same phenomenon is again seen as soon as the cells form the germ layers.

The polar differentiation runs parallel with the vital necessities of the cell. The free surface is that which originally stands in relation with the outside world. There the intake and output of metabolic products occur; there is found protection of the organism from harmful influences of the environment; on this surface develops the cuticle which (e.g., in the enamel) may reach great thickness. The basal side receives the nutritional material and the nerve stimulus. This side forms also such substances as join the cells firmly to the deeper elements. Since these topographical arrangements are always repeated in development the same polar differentiation is always repeated. It can, along with its consequences, be regarded as a constant feature in normal development.

We do not mean that this should be regarded as firmly fixed in the inheritance and that it was inherent in the cells as such. As in many other things the cells also can if, for example, placed experimentally in a different position, find expression, and if compelled to find a free surface turn the basal into a free surface. This naturally does not arise under ordinary conditions.

Free and basal surface can be joined by a principal axis (stereometric axis, cf. structural axis [para. 113] which, since it joins dissimilar surfaces, is heteropolar. Perpendicular to it are the other two axes which may be of equal or unequal length, and may join like or unlike poles, according as the cell is differentiated equally or unequally in length and breadth. Polar differentiation is clearest in the elements of the epithelial tissues, especially in the form with only one layer. The cylindrical cells of the gut epithelium are the best examples. In the single-layered flattened epithelium it can be seen with the peculiarity that the principal axis is very short, the subsidiary axes very long. In the many-layered epithelia the polarity is chiefly recognized in the deepest and the most superficial cells, whilst it is least obvious in the intermediate layers.

The effect of the polarity from a histological point of view is chiefly that the free and the basal surfaces exhibit typical differences. The free surface, according to the type of cell, is covered by cuticular border (enamel of the internal enamel cells), brush border, porous canals ; it develops the cilia, the flagella and stereocilia, also the specific differentiation into sense epithelium (sensory hairs, rods, cones). The cell products collect in the neighbourhood of the free surface of the cell (secretory granules, and droplets, e.g., zymogen granules). The basal side, on the contrary, is distinguished by the formation of the basement membrane. It may be that this is a product of the epithelial cell, or it may be that it is derived from the finest connective tissue fibrils. The epithelial tissue develops on the basal side of the cell simple fibrillary connections with the deeper structures. The basal side of the cell remains free in ordinary secretion, and only becomes filled when the secretion is extremely active. In gland epithelium the basal part shows only a slight differentiation into a granular or thread-like structure (basal granules). In a cylindrical cell the nucleus lies usually nearer the basal than the free border. The lateral surfaces of a polar differentiated cell are not perfectly indifferent to the polarization. The cells are separated from one another by intercellular spaces and join with one another across the spaces by protoplasmic connections. These intercellular structures are (in cylindrical epithelium) absent at the free ends of the cells ; these are joined with one another through the firmest bonds, the cement border.

All this is very important for the understanding of the organs. The free surface of the retina is opposed to the tapetum, the free surface of the lens to the lens epithelium, the free surface of the enamel against the dentine, the outer root sheath of the hair against the inner root sheath, whilst probably in the inner root sheath the free surface is represented by the outer (Huxley's) layer. The form of the gland epithelium is completely determined by the promorphology of the cells. The basal surface receives the blood and the nerve impulses. In the free portion the secretion collects and makes its exit to the exterior.

It is to be understood that this polar differentiation is not rigid but plastic, since the free surface can be extended, or it may be withdrawn into the cell with endoplasmic secretory granules, or that the lateral surface becomes the seat of formation of intercellular substances in the most active condition, the entire surface may become "free," and the secreting surfaces reduce the attached surface to a slender foot-like attachment, whilst all surfaces take part in the secretion (liver cells of higher mammals).

The promorphology helps us to understand the chorda dorsalis. The free surface of this, beginning as a ring-shaped organ, lies in continuity with the primitive gut, and the cavity is included in the interior of the chorda when its closure occurs where it remains only virtually present.

The basis of the chorda cells lies externally. This does not agree with the theory that the sheath of the chorda, with its fibrillary products, is a derivative of the epithelial elements, as has been accepted until recently. It has (Held) been actually shown that the sheath of the chorda, as ordinarily understood, has been derived from the connective tissue around the chorda.

The proof of the polarity of the deeper cells is not so clear. Where fibroblasts are sparse it can be shown that "free and basal," understood as referring to the matrix, are not without influence on the differentiation of the tissues. The most advantageous position for the differentiation of mesenchyme cells is always the basal surface of the epithelium. The oldest cells are therefore most extensive on the surface of the mother substance (e.g., surface of the cavity of the somite, the surface of the cœlom). The principal axes are directed from the cavity of the somite to the ectoderm and to the chorda, and from the visceral surface of the mesoderm to the entoderm, but the subsidiary axes are determined by the flattening of the cells. Fibril formation is always found in such cases first at the base, i.e., for example, between the chorda epithelium and the connective tissue cells. These cells are then pressed on the fibrils formed by them and (i.e., now where they are removed from the chorda) the younger cells are covered by a new layer of fibrils. This polar differentiation of the chorda sheath has been convincingly shown recently by Held. The subcutaneous tissue of fish and amphibia show a similar mode of formation. Especially do the fibrillar systems which cross each other in two directions at right angles suggest that the plastic capacity of connective tissue cells is affected in the direction of the two subsidiary axes (K. Rabl, fig. 57).

The polarity of connective tissue cannot yet be regarded as proven. Only in bony tissue do we meet again a striking differentiation of the osteoblasts in which the nucleus lies right at the basal border, whilst at the free end the plasma markedly accumulates and stands here in continuity with the bony substance recently formed, just as the enamel does with the adamantine substance (fig. 58).

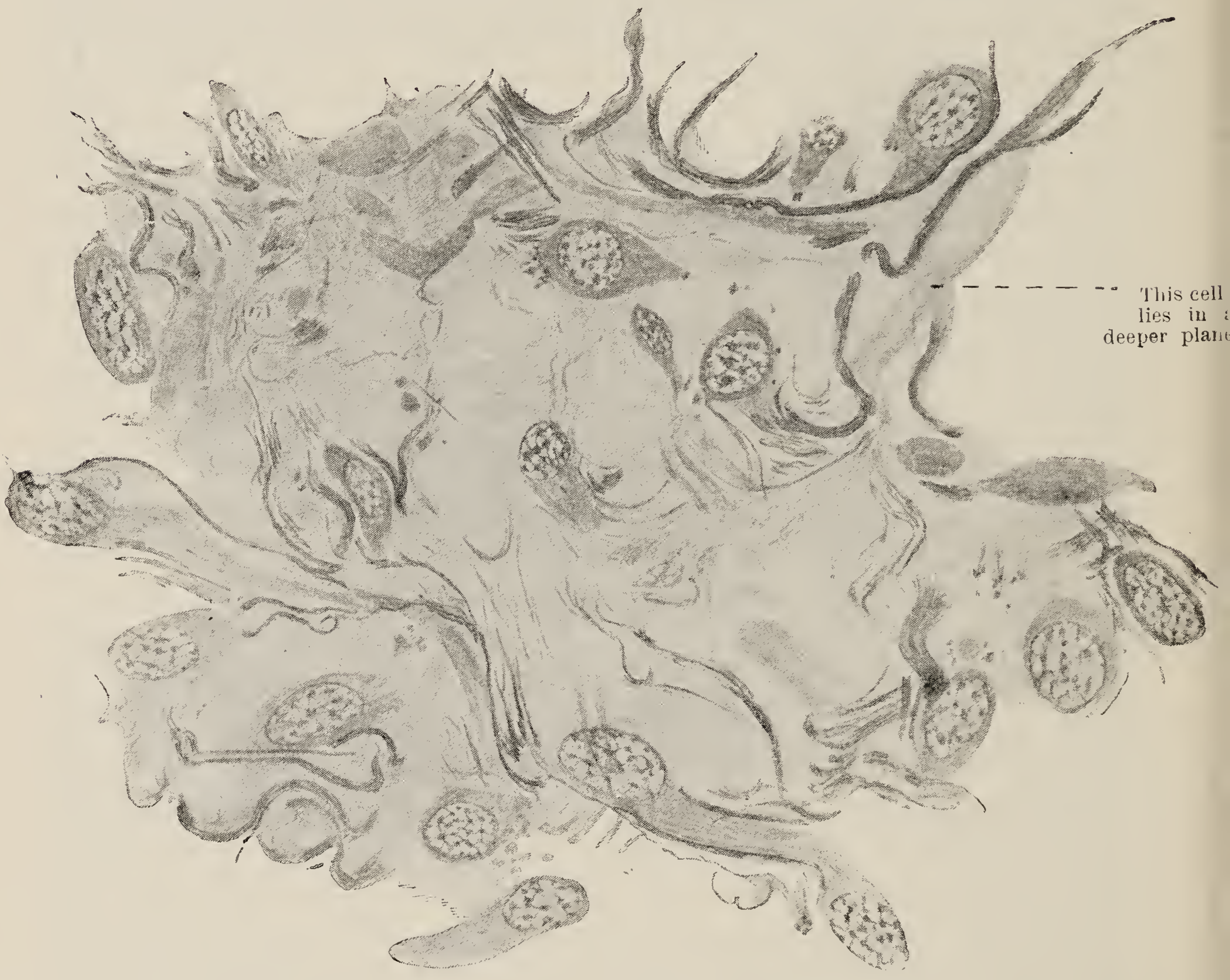

Fig. 57.—Embryonic connective tissue. Promorphological relation of connective tissue fibrillæ to the cells (see text). Where the cells are cut in their long axes there the fibrils can be seen; in transverse section of the cells the fibrils occur as points. These points can be followed as fine lines for a distance. Oblique sections show elongated fibril elements. Only one plane is drawn (on the right above the indicator line). The specimen is derived from the connective tissue of an embryo 20 cm. long of a cow. Fixed in sublimate trichloracetic, according to Heidenhain. Embedded in celloidin paraffin. Section through the decalcified hip-joint. Section 3 μ thick. Tissue of the embryonic sclera. Staining with azocarmine-anilin blue. The fibrils in the original preparation are light blue, nuclei and cell-bodies brick red. The nuclear structure in the drawing schematized by the use of the nodal points of the nuclear network. Enlargement 1 × 1,000. In reproduction reduced nine-tenths.

In muscle tissue polar differentiation is in part proven. The primitive condition of this tissue in invertebrates shows epithelial cells which give off fibrillæ from their basal surfaces (epithelial muscle cells). The transverse striated musculature of the vertebrate arises from the myotome. This possesses a wall and cavity. The cavity is a recess of the cœlom. The free surface of the epithelium of the wall lies in contact with the cavity, the base against the chorda and the neural tube.

At the base the motor nerves reach the epithelial cells, where they first form their fibrillæ (fig. 12*b*). These cells are therefore typical muscle cells. Later the individual epithelial cells grow in length in the direction of the subsidiary axes. With the increase of the nuclei arises a muscular column or muscle fibre, wherein the fibrillæ arise exclusively from the other surfaces of the muscle band.

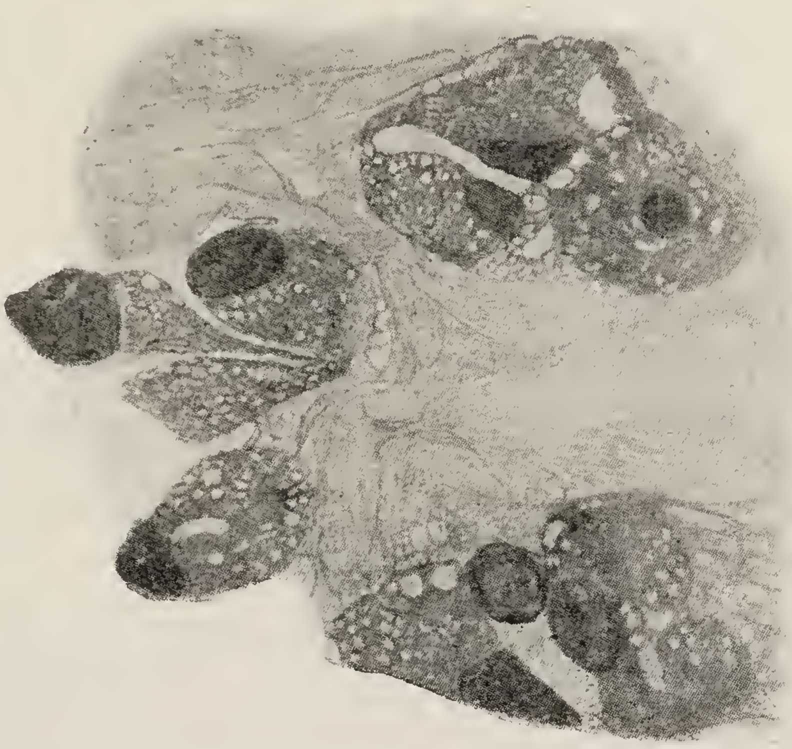

FIG. 58.—Promorphology of the osteoblasts. Explanation in the text (p. 336). The nucleus is everywhere pressed to the base as though forming a cap to the cell. The free end is in continuity with the bony-ground substance which shows a fine fibrillary form. The cells (on the right above, two cells visible) are everywhere surrounded by the bony-ground substance. At the lower border a clear space = blood-vessel with one red blood-corpuscle (filling the space above). Embryo of cow, 12 cm. crown rump length. The preparation is from the lower jaw and fixed in pot. bichromate and formalin. Embedded in celloidin paraffin. Longitudinal section of a portion of the posterior end of the primordium of the dentary. Section 3 μ thick. Stained with hæmatoxylin and acid fuchsin. Enlargement 1 : 960.

The sarcolemma is the later tubular differentiation arising from the development of the basal membrane of the epithelium (fig. 12,b).

The nervous tissue permits the recognition of polar differentiation in its earliest development. The free surface of the epithelium of the cells of the neural tube is turned towards the central canal and the ventricles of the brain. The nerve cells give off their principal process, the neurite, from the base.

They become multipolar as protoplasmic processes arise from the free surface. These might be compared promorphologically perhaps to the intercellular processes of epithelial cells. The unipolar ganglion cells are genetically bipolar, the processes if considered promorphologically demand that they should come from the free and basal surface. (On the spatial orientation of the neuroglia see pp. 332, 340.)

The observation of the promorphology of the tissue cells, which Hatschek first recognized and whose importance in histology K. Rabl first pointed out, affords the attentive observer rich rewards in the study of the textural formation of the body. As a far-reaching peculiarity it may be asserted that the epithelium arises quite differently from all other tissues in that the free surface affords the most important differentiation. All others (with the exception of the osteoblasts which therein stand nearest to the epithelial) differentiate from the basal surface (connective tissue, myofibrils, nerve processes). The name "apothelium" (in itself, meaningless) has been applied to this tissue.

(4) Connections of Tissue Cells.

Para. 98. If the tissue is a combination of similarly differentiated cells, then, after the problem of the form of differentiation, the problem of the mode of combination is the most important. The cellular doctrine leads often—and not only in what the science of histology is concerned with—to the erroneous view that the spatial separation of cells may be a necessary postulate for the existence of a

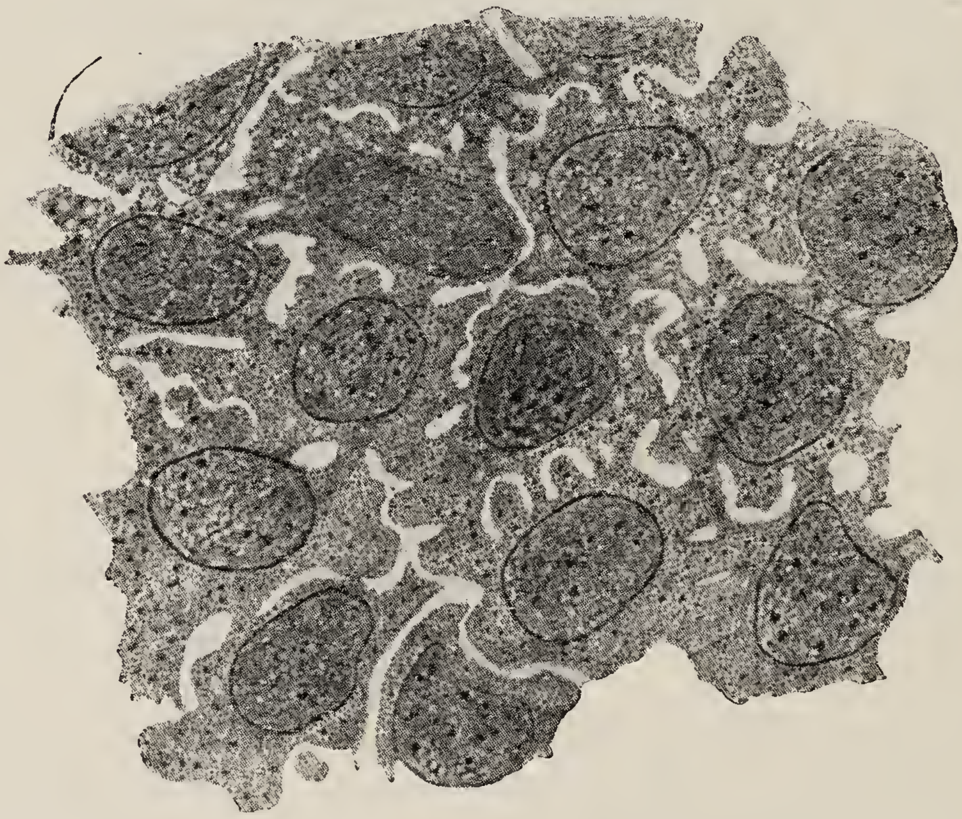

FIG. 59.—Broad cytodesmata between epithelial cells. Where these appear to end freely the connections lie in other planes (higher, deeper), since the thickness of the section shows only one optical plane. Taken from the epithelial covering of a gill plate of an axolotl 14 cm. long. Fixation in strong Flemming solution. Staining of all the gill arches before removal of the skin in alcoholic hæmatoxylin according to Oscar Schultze. The larger nodes in the nucleus are real. Finer nuclear and plasmatic structure schematic. Enlargement 1:733. Nine-tenths reduced in reproduction.

science of cells. The facts suggest the contrary. For the existence of a science of cells it is of no decisive influence that the individual cells are often joined continuously with one another.

The dividing cells may continue in relation with one another through plasmatic connections (Hammar). It is not certainly known if and how long these are retained, and if these processes later become the cell connections.

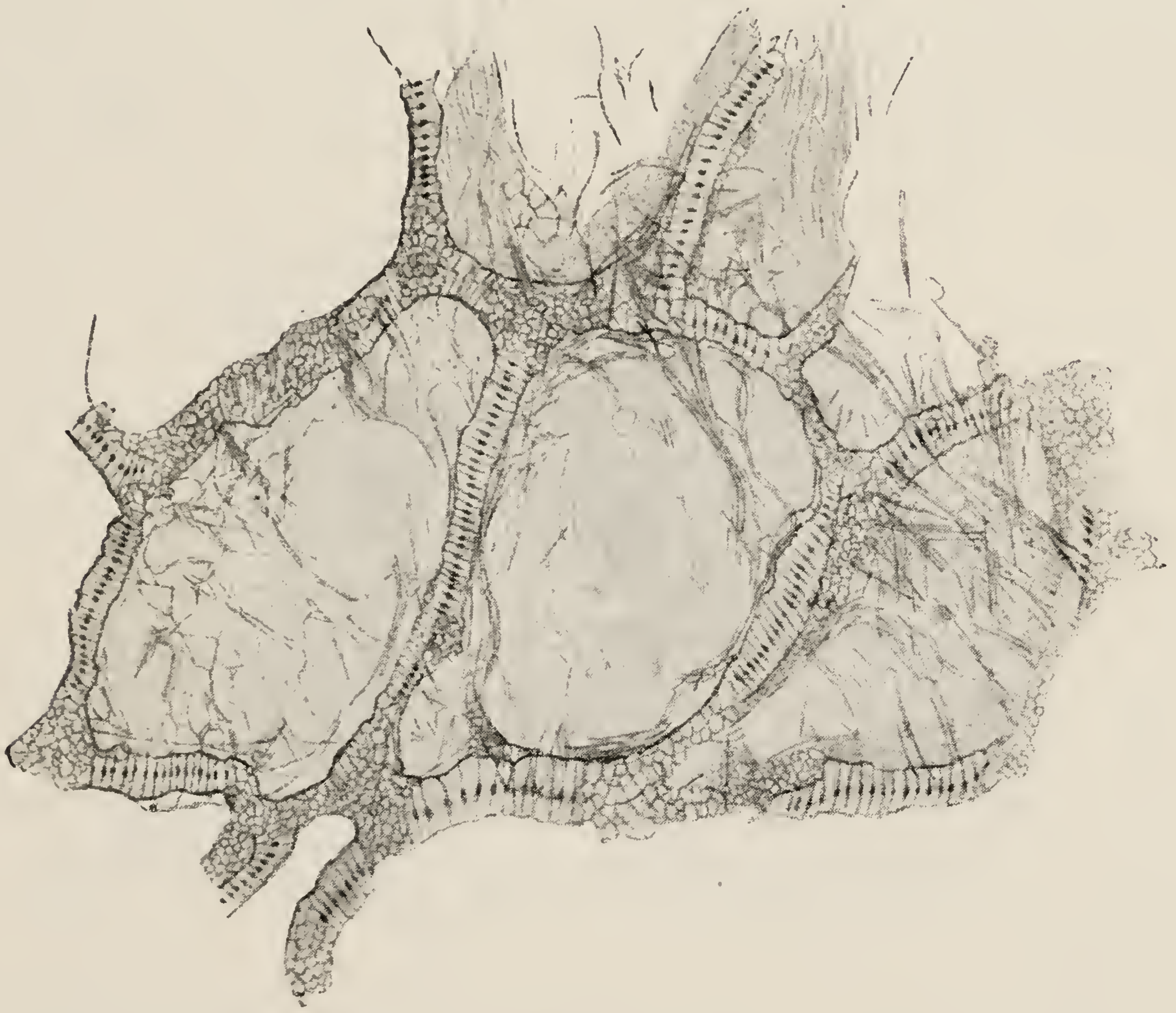

FIG. 60.—Intercellular structures and tonofibrils of the epithelium. Four whole cells and parts of others drawn. No nuclei present in the plane drawn. The nuclear zone is indicated in the two largest cells by the clear area in the middle. The fibrils are actual, likewise the cytodesmata. Places cut tangentially show that these are alveolar and not thread-like. The knots in them, which are easily recognized in the preparation, are schematized. The passage of fibrils through the cytodesmata from one cell to another can, despite the section thickness of only 2 μ, be followed only here and there. At some points the passage is visible. Embryo of a cow, 20 cm. crown-rump length. A portion of the primordium of the hoof of the terminal phalanx fixed in sublimate-trichloracetic acid according to Heidenhain. Embedded in celloidin-paraffin. Thickness of section 2 μ. The cells lie in the middle of the many-layered stratum granulosum of the epidermis. Stained with iron hæmatoxylin according to Heidenhain. Magnification × 1200.

They are of twofold origin:—

The one (primary) is to be referred to the division of the tissue cells through which the cells are not perfectly separated from one another. The others (secondary) are certainly new formations. Each is found especially in the elements of the epithelial and supporting tissues, especially also the nervous tissues, whilst the muscle tissues (with the exception of the tissue of the heart musculature of mammals and the connections of the striped muscle fibres with the tendon fibrillæ) have no intercellular connection of their elements.

Primary connections: The epithelial cells are joined to one another by strong processes, which have been described according to their nature as cytodesma or plasmodesma (Studnitzka: cytodesma arise from ectoderm and endoplasm, plasmodesma from endoplasm). Though these intercellular structures are often markedly reduced, especially undergoing reduction through the close compression of the cells, they yet form a characteristic feature of epithelial tissue (fig.59). This becomes especially evident when the epithelial tissue starts some unusual development, e.g., growths like polypi and condylomata. Also, under normal conditions, when a limited metamorphosis may occur at some point. In cases such as these the intervals between the cells increase (fig. 61) and these appear, since part of their connection is retained, as branched elements standing in relation with one another, between which drops of an intercellular fluid are found (enamel pulp of the tooth germ, mucous membrane of the fœtal ear).

The metamorphosed epithelial tissues possess great similarity with embryonic connective tissue. The neuroglial elements are also epithelial cells modified in a special way. Between their processes nerve cells and nerve fibres lie. In the neuroglial cells fibres arise (epithelial fibres) which, of course, have been demonstrated in the epithelium, especially in the flattened types (fig. 60). They are of an endoplasmatic nature, and become continuous through the intercellular connections, therefore continuous through the whole thickness of the epithelium. They transform such an epithelium into an especially strong band, which may subserve stimulus conduction or mechanical needs. In mechanical needs (stiffening of the epithelium, a displacement), one sees the real reason of the fibrillæ (tonus fibrillæ).

The significance of the intercellular spaces as places of deposit (for nerves, pigment cells), or for continuous movement (for wandering leucocytes) is to be appreciated, as well as the significance of the intercellular bridges (fig. 61).

The embryonic connective tissue is the primitive form of connective tissue. In invertebrate animals it forms the continuous basic substance. Its continuity with the epithelial tissue it retains at the points of its derivation from it, as the investigations and figures of Schuberg have shown.

Its functional value lies in the jelly-like nature of the tissue, in part in the turgor of the coagulated fluid present between the cells (hence the name jelly tissue) (fig. 62). The cells retain their connections, which, so long as they can be seen, show great complexity and can hardly be reduced to any scheme (Schuberg).

These connections need not be represented entirely as bonds, but also as flattened elements overlapping, arching, and dividing, so that there is formed a three-dimensional net with besides three-dimensional spaces running between the cells. This was known to the older anatomists [Rauber], and has again recently been described [Huek]. According to the proportion of plasmatic and intercellular substance, the net may be broad and extensive with narrow intercellular spaces, e.g., in the region of first centres of ossification, or the connections may be fine and sharp—spun out of fine threads with broad intercellular spaces. Also in tissues which arise from embryonic connective tissue the intercellular connections persist (reticular tissue [fig. 63], cartilage and bony tissue). If the cells remain in connection with one another, in loose, fibrous connective tissue, remains an open question. This is often affirmed and often denied, and it is said that our defective technique is unable to settle the matter. For some cases the use of special methods and of dark ground illumination more certainly brings out the connection (p. 346).

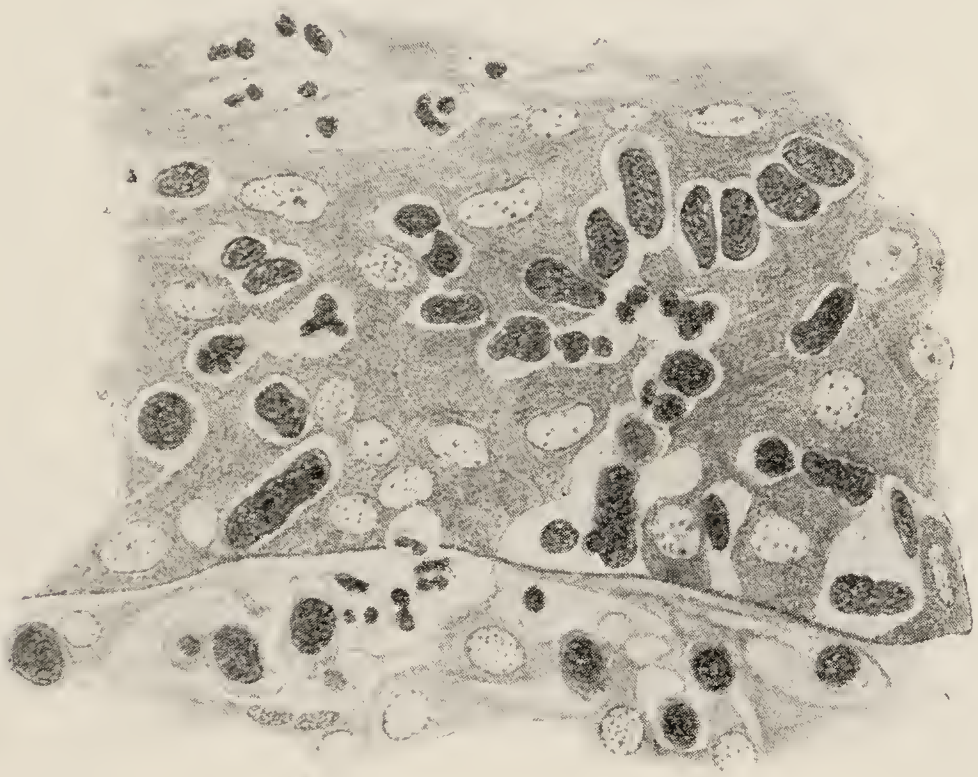

FIG. 61.—Lymphocytes in broad intercellular spaces in stratified epithelium. Tonsil of a 4-day-old dog. Fixed in Zenker's fluid. Stained with hæmalum. Embedded in paraffin. Thickness 7·5 μ. Magnification × 750.

The question of continuity is a burning one in the case of nerve cells. It is here of fundamental importance; its essence depends on the intercellular connections. If we think that the integrated activity of all cell elements, or at least of the larger cell associations, is valuable for the maintenance of vital processes, then this must be carried out either by nervous paths as in muscle tissue, thus achieving an integrated function without any plasmatic connections, or the elements themselves must remain in functional connection with one

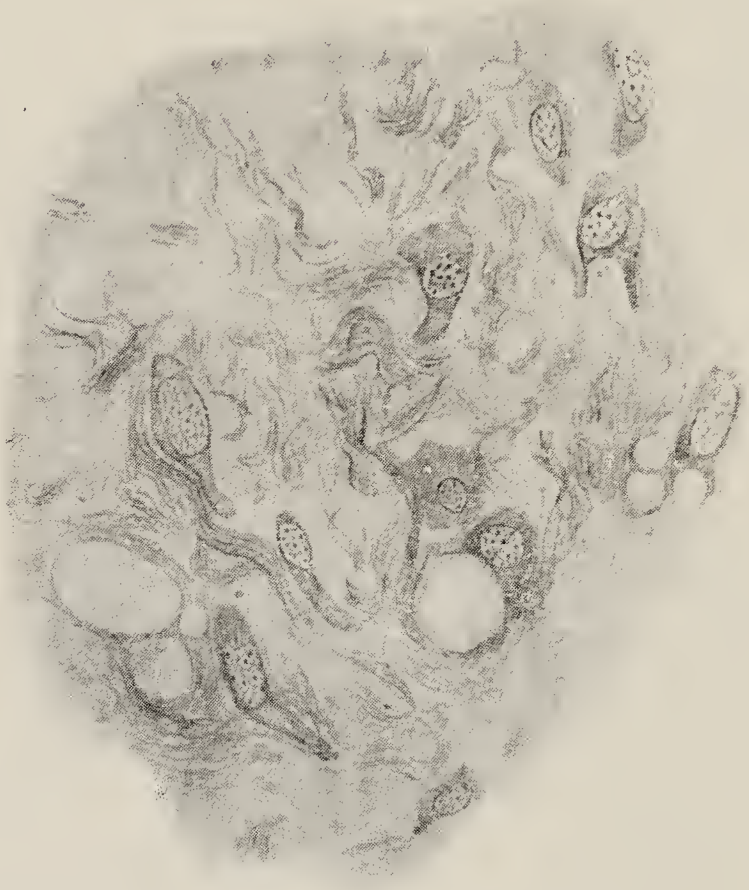

FIG. 62.—Young mesenchyme (mucinous connective tissue, umbilical cord). Fibrils surrounding the cells. Through separation arising in the colloid intercellular substance, vacuoles with a clear fluid content develop while the more tenacious fluid elements form the firm ground substance (exoplasm) around the cells. Embryo of a cow 20 cm. crown-rump length. Umbilical cord fixed in sublimate-trichloracetic acid according to Heidenhain. Embedded in celloidin-paraffin. Thickness of the sections 5 μ. Staining in azocarmine-aniline-blue according to Heidenhain. In the original preparation, cells and ground substance reddish, nuclei brick red, fibrils light blue. One plane is drawn. Magnification × 650.

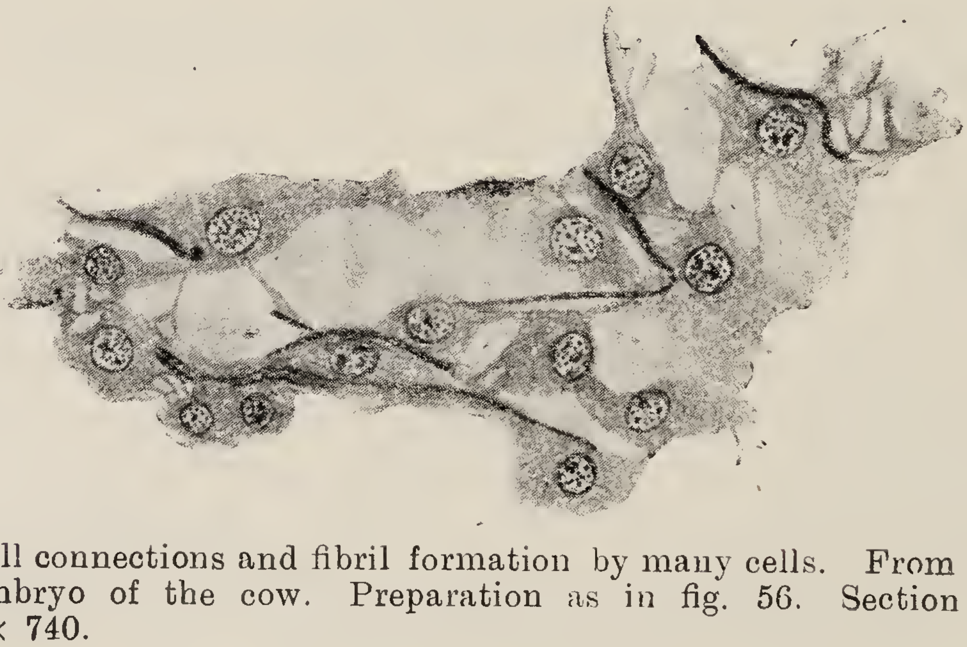

FIG. 63.—Cell connections and fibril formation by many cells. From the spleen of a 20 cm. long embryo of the cow. Preparation as in fig. 56. Section thickness 3 μ. Magnification × 740.

another. The intercellular connections of the vegetative cells stand obviously in the service of such an immediate transference of stimulus which subserves especially well the integration of the function.

A continuity of cells is present in nervous tissue for the purpose of stimulus conduction and stimulus transference.

The neuron doctrine in its original form denies this and admits only a functional contact. Early in the medullary tube the neuroblasts become perfectly free from one another, and do not remain in connection by intercellular bridges with one another like the epithelium (His, in Rabl). To accept an analogy between intercellular bridges and dendrites is unwarranted. Physiology supports the contact doctrine and not the idea of continuity (cf. in Heidenhain). Anatomical investigation can support the idea of continuity (Held). Through the most delicate technique it has been proven that, for example, the Purkinje cells of the cerebellar cortex are quite certainly continuous through their dendrites [Stöhr, junior].

The neuron theory is, of course, no more ruled out by these and similar remarks in the anatomical sense than the cell theory is demolished by our growing conviction of the inter-connection of all cells [see below, para. 99].

Connections for the conduction of stimuli are not unknown in muscle tissue, as the structure of heart muscle shows, in which the original transverse striated muscle cells develop in syncytial connection (heart muscle cells with transverse striated fibrillæ). The functional significance of this is now quite clear; it has become especially clear through the presence of these stimuli-conducting bundles.

All these intercellular connections have this in common, that they are present within the same tissues, and are to be referred directly to the divisions of the stem cells. It is worthy of note that cells which have no genealogical relationship with one another may develop such connections. This has been well known for some time.

Para. 99. These secondary connections are present between the germ layers before the migration of the mesenchyme cells from the mesodermal epithelium of the middle layer takes place (and in part from the outer layer, cf. above). This is seen between the ectoderm and myotome, between myotome and neural tube, between chorda and myotome, etc.

Primarily these fine protoplasmic fibres cannot be seen since they first arise in the course of development in the neighbourhood of primitive organs which they join to one another. We have therefore to look on them as new formations. They have been given the name of "epithelial connective tissue." Their significance is extraordinarily great. Functionally they exhibit a complete conduction system for stimuli. Genetically they correspond perfectly with the plasmodesma of Hensen and Gegenbaur for the development of nerves. This name, "plasmodesma," ought now to be limited to the primary connection (Studnitzka). Morphologically they represent paths along which the later elements of the mesenchyme, especially the developing nerve paths, will grow (Held). Histologically they are probably the starting point of all those connections by which the different tissues of the body are joined together.

It might well be observed that in most textbooks this continuity is only briefly mentioned and thus their real significance is obscured. The epithelial tissue is joined with the deeper tissue by fibrils which ascend from the deeper structures and there form a limiting layer. With this the epithelial cells are firmly joined. Also fine fibres radiate between the cylindrical cells (Weidenreich) of the rete Malpighi and end in the borders of these cells. In amphibia such connections are very clear (Schuberg). Epithelial cells forming processes have certainly been observed in mammals (Mollier, cf. also Hoepke).

Continuity arises between the striated muscle fibres and the tendon tissues in which the striated fibrillæ of the muscle become continuous with the fibrillæ of the tendon (O. Schultze, Schaffer, Sobotta). This can only be referred to a secondary plasmatic continuity between myoblasts and mesenchyme cells within which continuous fibrillæ are differentiated. These become contractile in the muscle fibre, collagenous in the tendon and indifferent in the transition area (Schaffer, p. 204). Continuity arises between nerve and muscle tissue. The neurilemma of the nerve becomes transformed into the sarcolemma of the muscle fibre, the neuroplasm into sarcoplasm. The endplate of the nerve lies in an extensive accumulation of the latter.

If we survey these arrangements as a whole we realize in a more comprehensive way the unity of the body. The usual presentations in textbooks of histology are based on the principle that the cells are "building stones" piled one on the other. This has had the result that the opposite, so easy of proof, is described as new and is used for criticism of the cell doctrine (p. 354). One is led indeed to regard the old conception of Rauber as correct, that it is not the combination of the elements that is unusual and needs explanation, but their perfect isolation. We must now see if there are perfectly isolated elements in the body. The free cells of the blood and the lymphocytes in the lymphoid organs are such; the wandering cells of connective tissues, the sex cells in the beginning of their development and also at the end of maturation are such (in the intermediate stages they are related to the follicle cells and to the cells of Sertoli);

perhaps also the smooth muscle cells in so far as they are not reached by processes of sympathetic and parasympathetic nerves (Schaffer, p. 267).

Isolated organs are extremely few, since they are all invested by connective tissue and this is continuous at their surfaces. In respect to actual discontinuous relations in the body compare the statements above on the cavities and spaces.

The histological relationship is therefore the one typical of the body. One might well give space to the idea that the destruction of this relationship, the absolving of a tissue from all the regulating influences, leads to an abnormal behaviour. This may be the starting point of tumour formation.

(5) The Microscope, Microscopic Technique, Possibilities and Limits of Objective Investigation of Tissues.

Para. 100. The discovery and perfection of the microscope and the submission of the elements of the living body to microscopic investigation have been the means by which the study of the tissues has reached its present position. From the standpoint of Goethe, that the nature of man can only be investigated so far as man himself can employ the organs of nature, this whole kingdom would remain unclaimed. And yet is this standpoint not incorrect when we say that man can arrive at an actual objective knowledge of the properties of nature only through his senses. Naturally the subjective limitations of all knowledge apply here [para. 8]. But yet these limits are essentially other than those which we erect between our eyes and nature through the use of optical instruments and the preparation of the living object. We are so strongly affected by the conduction of our eyes that it appears as if they were pressed right on the elementary parts of the object. But do we actually see the object itself and do we see it free from misleading forms and can we see it free from such?

All these questions we must deny; we accordingly accept the science of the finer form of the body as being of no value, but we sharpen our appreciation of the fact that with this step from the gross preparations to the microscopic consideration we enter an area in which the rules of observation and judgment are unknown. We are up against the source of failure in the technical preparations of the objects. A nerve followed to its finest branches by the unaided eye or by a lens is and remains a true observation. As soon as a nerve is impregnated with silver and observed under the microscope there is a result, but we do not know in what state we must regard a "nerve" which we have impregnated.

One can go further than a successful impregnation allows. All that is impregnated need not be nerve. The history of the investigation of the finer form of the nervous system and its development affords numerous examples of warning. In histology the criticism of the method and the comparison of the results obtained by various methods play a rôle which does not exist in the case of the study of the corpse. However, the most exacting criticism can only demonstrate what the form obtained most closely resembles in nature. The science is exact when it arrives at an agreement with other methods. We must examine these other methods and see if they arrive at different conclusions on the last questions of cells and tissues. For proof of the latter [para. 117] it may be here only noted that the tissue as a colloid becomes changed when subjected to alcohol and xylol.

The investigation, without alcohol, by embedding in special gelatine solution, and investigation of frozen sections of such blocks in gelatine balsam in the dark-ground field, has shown remarkable differences (Heringa, p. 286).

Of the theories of staining the physical chemical has long had the preference (Michaelis, 1910, lately advanced again by v. Möllendorf, 1923). The dye-stuffs are colloidal solutions; the particles of the stain are suspended particles which press into the gelatine with varying intensity according to the stain. The structure of the fixed tissues is of varying thicknesses; the thicker the structure the more difficult the penetration of the stain and the more difficult still is it to get out any of the stain which has penetrated. The effect of the stain is the product of these two factors. Stains that diffuse with difficulty (large colloids) bring out the most different staining the longer they are in action. The thickest structures are the last to stain. The final result is that staining is a process of adsorption, that is, the dissolved stain extends on the surface between two phases in the colloid chemical sense (Michaelis, p. 436). The old chemical theory has now very limited application. It is now admitted (Michaelis l.c. Heidenhain, Pflüger, Archiv, vol. 100). Above all it still appears to play a rôle in fundamental and important staining, viz., that of the nucleus. The nuclei are distinguished by the presence of chromatin in combination with a phosphorized organic acid, nucleic acid, and always show an elective chemical staining (with basic dye-stuffs). Also other tissue substances (calcium salts, elastin, chondromucoid of the cartilage substance, mucus) possess chemical affinities for special dye-stuffs. The staining here is certainly a microchemical reaction. Colloid chemistry on the other hand would not provide information on the chemistry of these structures but on their thickness. Microchemical reactions are known for calcium, iron, and recently for nucleic acid.

What, however, do we see through the microscope? Certainly not the object itself. The processes which make objects visible under the microscope are unusual in that the object itself is not luminous. It must be illuminated from some source of light and thus each particle in the object becomes a source of light which spreads in all directions. What arrives at the front lens of the objective is not like the real image formed when light rays are brought to a focus by a lens, but a pencil of rays bent according to the laws of refraction and interference. We see only the images formed by these bent rays. The lateral rays do not arrive in the microscope. The real image produced by the objective (in the tube of the microscope) is not an image of the object but a system of bent images which arrange themselves around an axial centre composed of unbent rays. These unbent rays we do not see, so indeed the microscopic view rests on what is produced by the bent images (secondary nature of microscopic images, E. Abbé).

Through this theory of microscopic images are determined also the limits of what we can perceive generally by the aid of the microscope.

The "magnification" of the microscope depends on the resolution of the structures by the lens of the objective and the enlargement of the bent images produced by the objective by means of the ocular system. The resolution of the objective system (often wrongly called by beginners the magnification) rests on this, that the structures lying side by side in the three dimensions of space provide as such real bent images above the objective. The larger structures separated from one another by considerable distances (a network with wide spaces) are resolved by a feeble objective (that is, the greater the focal distance the smaller the angle of entrance). The bent images arising here are numerous and lie close to one another. The finer the structure we wish to see, the closer, therefore, the structural net made by the source of light illuminating it becomes, and therefore the stronger the lens that must be used, i.e., the shorter the focal length the larger the angle of entrance (the sine of half the angle of opening multiplied by the refractive index of the immersion fluid [cedar oil] is known as the numerical aperture). The bent images are then situated at the greatest distance from one another and arrive at the aperture of the lens of the objective in the smallest number. With the strongest lens special means of illumination and the introduction of the immersion fluid into the space between the objective and the cover glass in order to get the best of the image are needed. If the structure becomes so close that it occupies not more than half the wave-length of uniform white light, then the bent bundles of rays are so far from one another that their direction will no longer bring them into the microscope. Structures of this form with a size of $\frac{2}{10}$ micron (1 micron $= 1\mu = \frac{1}{1000}$ mm.) cannot be recognized by the human eye through a microscope. The size of the molecule lies still three decimal places below this size (cf. the description in Schaffer).

This limitation can be raised by other means (ultramicroscope, p. 384). Here elements of the size of molecules are made visible.

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(IV) Cytomorphology and Leptonomorphology.

Para. 101. Differing from the usual presentations which take their starting point from the cells, the presentation of the morphology of the cells here forms the conclusion of the building of our science. The presentation in which the facts of cytology are elucidated with perfect pictures right at the beginning has its didactic justification because the beginner must be furnished at one time with the elementary facts. If, however, the orbit of the questions related to morphological science is traversed, then one returns to the elementary organism in order to see how far from their structure explanations are to be expected on the basal questions of the science of form. There will be discussed here not so much the individual facts of cell form but rather those questions will be dealt with which arise from the cell theory in anatomical science as a whole. Two problems arise here, one depending on the conception of the cell as the structural unit and the other on those phenomena which arise when the cell is considered as an elementary organism. They both belong to cell morphology. The study of the finer form comes later.

(A) Cytomorphology.

(1) The Cell as the Tissue Unit.

(a) The Cell Theory.

Para. 102. As the founders of the cell theory had demonstrated that the body is a combination of elementary organisms, and as embryology had shown that every organism in the beginning arises from only one cell, it was not surprising what a great significance the cell theory would come in time to possess in the understanding of vital processes. The physiologist was slow to take up the idea (Verworn) of studying the vital processes in the cell itself. In so far as it was included in the older pathology (Virchow) the cell theory was always in being, but it was not yet creative in the strict sense. There was first need of the discovery of the phenomena of fertilization (O. Hertwig) and the discovery of indirect cell division (van Beneden, K. Rabl), by which not only was the investigation of the chromosomes introduced, but also the first steps appeared combining the phenomena of form with the cell processes. In this way it became possible later to give a cell basis to the investigation of heredity. The science is now in the middle of the struggle to combine the morphology of cells with the phenomena of the change of form and the origin of species. The old investigations which sought to explain the finer form of cells are now proceeding along most fruitful paths through the knowledge of colloidal form of the cell and the nuclear protoplasm, so that Koelliker's hope of a " discoverer of the origin of the cell who would obtain greater renown than the discoverer of the cell itself " is brought nearer to fulfilment. It may be anticipated that before the end of the first hundred years of cell investigation (1938) this step will be possible, which will carry us to the physical, chemical and physiological relations of the cell. The reader who desires some idea of the present boundaries and content of cytology may find it in the work of Lundegardh and Tischler on plant cells and plant cell nuclei. This completes the great work of Heidenhain for animal cells, and further, in respect to the great mass of material added since the work (1908) of Heidenhain, far exceeds it. Not only cytology but also the study of the nucleus (Tischler) has become a science of its own with a colossal literature.

In view of the results that immediately flow from the significance of the cell theory it is a duty to mention that this significance has been denied. There are three reasons for this denial; to recognize them is essential for the understanding of recent controversies.

(1) The primacy of the cell has been contested first with reference to its granular form. These granules have been regarded not only as living but even in such a way that the cells may not be the last living element. Just as the body is formed from cells so the cells must be formed from granules (Schlater). He argues for the belief that, speaking phylogenetically and by a bold extension of the word "phylogeny," to include all possible ancestral organisms, the cells may arise from granules. On the contrary, we know of no example where a cell arises from something not a cell. Cells are always present and always arise from cells. There the conclusion is misleading and the comparison false. That organisms arise only from cells, and that they do arise from cells, we know because we see it, and because unicellular organisms which we might use as hypothetical evidence we actually know as individuals. Of the cells we only know that they contain granules. If these might be the living elements of cells as is probable, yet they are never found outside the cell and are present in the absence of a cell; it was humanly intelligible to suppose that the parts of a cell might be related to the cell in the same way as the cell to the organism. But all that we know up till now of the organization of cells impresses us only with the inconceivably complicated organization of these most recent and special elementary organisms. Nothing suggests that a cell can arise from the mere packing together of granules.

(2) In the second case the criticism of the cell theory starts from the idea of an independent life of the intercellular substance. This goes so far as to ignore the cells and to speak of "living mass," while the physiologist with a complete disregard of the cell speaks of "living substance" (pp. 38, 39), which naturally does not exist because it is only present in the form of cells. It will not be denied that many things suggest most strongly the individual life of the intercellular substance. It represents an advance on the old opinion, according to which these substances played throughout a passive rôle. It is necessary to get a clear idea here of what one means generally by the notion of the "life of the intercellular substance."

The idea that the ground substance is alive is especially to be referred to the double implication of the conception of life already mentioned (p. 34), dead and not living. The question is best seen in regard to the ground substance whether it be living or non-living. Dead (destroyed) substances within the body, so long as the body is healthy, undergo disappearance and absorption or excretion. Since all intercellular substances in the last resort are derived from cells, the question can only be, whether they suffer such an enfeeblement of the capacity to live, that they become changed to the state of non-living crystals, salts, stone. This is difficult to accept. The derivation of fibrillæ for example, and their increase, or the division of the fibrillæ present, takes for granted the growth, nutrition, metabolism. In this sense the question of the life of intercellular substances can never be the subject of criticism. The position of the question would be different if one knew that the ground substance possessed a life independent of the cells as is indicated by the expression "living mass." Then it might be said that the conception of life need not be bound to the cell, but rather that life objectively occurs at one time in the cell and at another in the intercellular substance. From the standpoint of our declarations on the conception of life it is necessary to prove, since the proof has not been furnished hitherto, that some extracellular formation possesses all the nine characteristics of life [para. 13]. It has been possible to show this in the case of cells. All the investigation of living cultures, outside the cell, has shown that extracellular forms are only capable of living in relation with cells.

The views now widely held on the formation of the ground substance make this quite understandable. The above criticism overlooks the relationship of the ground substance. Every ground substance is an exoplasmic formation continuous with the cell (fig 64).

Its substance, spatially separated from the rest of the cell, appears therefore, in so far as it is apparent in the complicated exoplasm, to be either in the cells or at least connected with the cells. The living phenomena which the cell remnant exhibits to us, e.g., connective tissue cells, are, of course, the minima of life which, compared with the ground substance, are extraordinarily violent and stormy. The reactions to mechanical stimuli affect the ground substance as might be expected and not the cell remnant. It however does not follow from this that the reaction is independent of the cells, still less that the reaction does not affect the protoplasm and nucleus.

For a long time the chorda sheath has been used as a stock example of a fibril formation without cells.

Since this example has now been rejected (Held) there is only this to say, that the appearances of life in the cells of the ground substance reach far beyond the cell protoplasm, that the ground substance is consequently only an indicator of the life of the cells.

How far reaching these effects of the cell life are is shown by the complicated formative processes in the chitin skeleton of the insects. These chitinous layers stand in relation with the matrix cells as massively developed cuticula. To believe that these cuticular formations have their own life would be as reasonable, for example, as to believe in the separate life of a nerve-ending because this is removed so far from the ganglion cell.

In botany the cell theory has never been attacked because the one exoplasm of the plant, the cellulose membrane, shows clearly the phenomena of life, but there can be no doubt of its dependence on the cells. It suffices therefore to demonstrate that in animals one side of the activity of the cell, namely, the production of exoplasm, which depends on the cell, plays a very much greater rôle than in plants. This life of the ground substance, which we must understand as dependent on the cell, used therefore not to be described as "inborn." It is the latest activity of the cell.

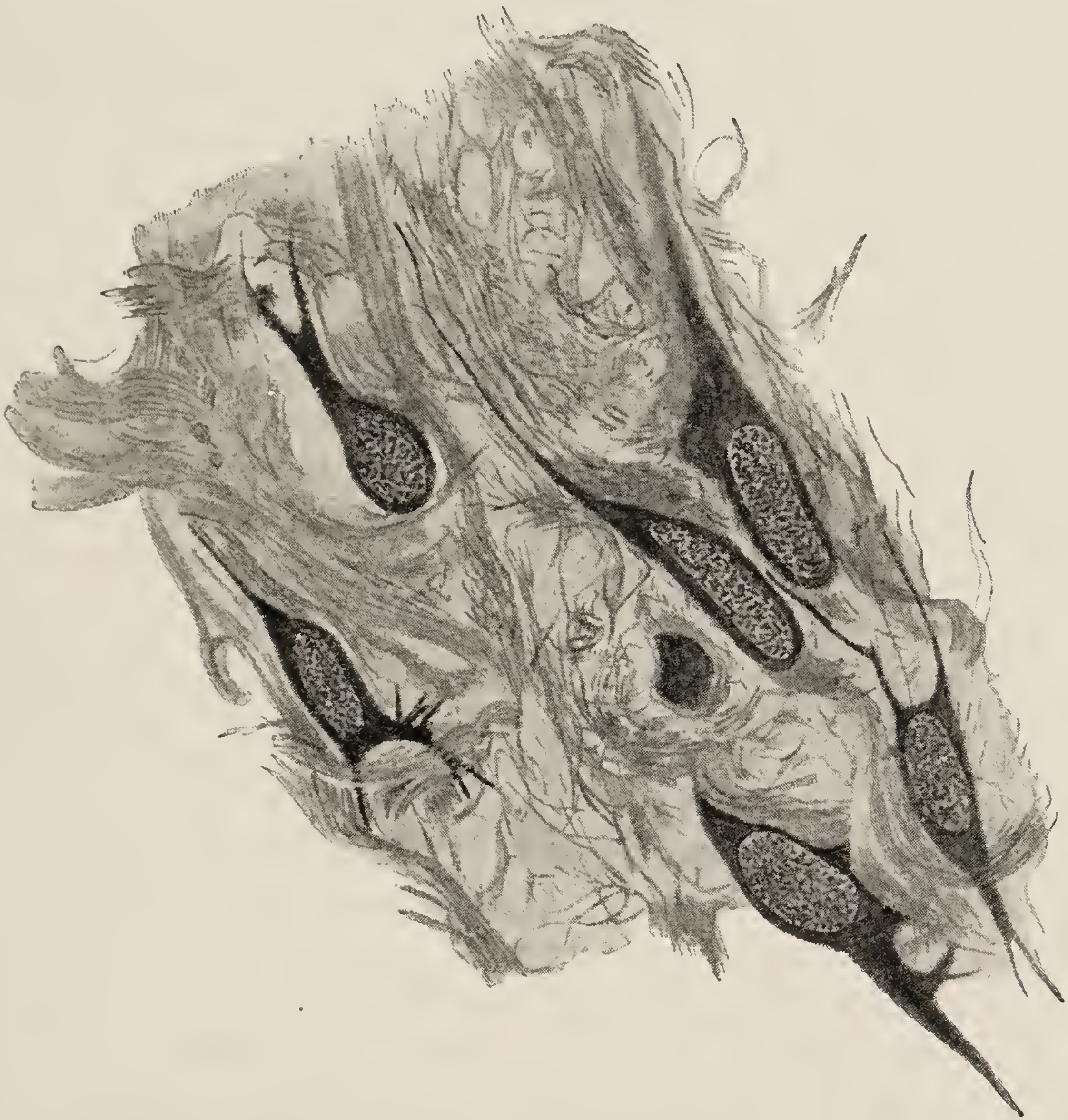

Fig. 64.—Connective tissue in connection with exoplasm and fibrils. From the intervertebral foramen of a 14 cm. long axolotl larva. Portion of the trunk segment fixed in sublimate-trichloracetic acid according to Heidenhain. Embedded in celloidin-paraffin. Thickness of sections 7·5 μ. Staining in dahlia according to Schuberg. Magnification × 733.

(3) The acceptance of the cell theory is finally supported by the facts of cell connections (cf. the most recent presentation of Huek and the older of Rabl). So far as the facts are concerned they have already been presented [para. 98]. Here may be mentioned only the historical, actual and theoretical difficulties in which one is involved in the present form of the cellular doctrine, as it is usually stated in relation to "the conception of the whole." No one denied that there is only a life of the whole, only a disease of the whole,

as well as a life of the cell, and a disease of the cell. Clinical experience (Kraus) teaches that in a kidney disease not only the kidney cells but the whole man is sick. A good deal of physiology shows also that one must start not from the life of the cell but from the life of the whole, which may be more and something other than the sum of the life of the cells. Also, developmentally, the body may not be the product of cells but an individual whole, which may be subdivided cellularly (the whole forms the cells, not the cells the whole).

In a historical review we might expect to see in the present state of knowledge something new, but already Virchow (Cellular Pathology, Chapter I, p. 15, Chapter XIV, p. 263 and following) has noted these twofold implications of what may be living. The essence of the cell theory is not that the cells have their own life, but that besides the life of the whole there may be special foci of life (diffuse) and "that in no way, so far as our experience goes, does there exist a single anatomical centre from which the activity of the body is conducted in a recognizable fashion." Actually things are now otherwise. In consequence of the enormous progress in detail it is now proven that there is "no anatomical centre" from which the "whole" inaugurates the activity of the elementary life-group centres. One, earlier, might have suggested such an activating centre in the nervous system or in the blood ; now one could see it in ferments, antibodies, enzymes, hormones and the sympathetic system. Always the anatomist will refer these effects back to the cells of the blood-cells of the ductless glands, ganglion cells of the sympathetic, whose function is again governed by other vital groups. The fibres of the labyrinth run only from cell to cell, they never run to "the whole." Again, the humoral theory often comes to the front, but again it is a cellular mechanism, since all "humours" are derived from cells. Any relation to the humoral theory of the ancients is perfectly excluded by this fact. We have only proceeded further in this matter in that we know exactly the development of the body from type-cells provided with a specific inherited constitution, and accordingly we know that constitutional injury can and must affect the whole since the defective primordium is carried into the development of many if not all the elements. Also, theoretically, Virchow has (loc. cit., p. 265) clearly perceived the fact when he says that unity only arises in our conciousness [cf., our remarks, para. 14]. This has lately been quite properly emphasized by an author (Zimmermann), however, with the erroneous conclusion, that he now denies the empirical presence of a "unity" (whole). This is false. The "unity" really exists ; but empirically can only be investigated in the dependence of the parts on one another. The recent opposition to the cell theory starts, therefore, from very old, long-known and correctly appreciated facts. It does not enrich our knowledge, certainly on no scientific question, but it offers a metaphysical transition for our consideration by which each can contain the other. Whether an effect of the whole on the part is to be regarded as a cause, that is, if the whole function is not the sum of the functions of the parts, if it physiologically depends on a plasma behaving as an entity (Lundegardh), more detailed physiological investigation is necessary to decide.

(b) The Cellular Doctrine.

Para. 103. The relation of the cell to the whole, Virchow described in the following way (p. 15) :—

> The character and unity of life cannot be found at any single point of a higher organization, e.g., in the brain of man, but only in the definite, constantly restored orientation each individual element bears in itself. So it happens that the integration of the body, the so-called individual, takes the form always of a common direction and forms an organism of the social type. A mass of separate existences have become related to one another, so that each element has a particular function and each, when its function becomes harmonized with the functions of the rest, has still gone on with its own particular function.

This definition is better than the much used description of the cell-state. All objections which one can make against the comparison of the cell state are at once met by the above. Since the body is a "type of social organization" and the cells work in harmony with the functions of cells or other parts, their functions can start from within themselves. To all this there can be no objection. Yet the comparison of the cell state appears to us of value as it is now generally applied. With its many implications (division of labour, differentiation, hierarchy of function, social good, defence, sacrifice, subordination, disease, tumour formation), it is so illuminating that we must plead for its preservation. The objections which have been urged against its excellence are worth noticing but are not of great moment. They are two. The combination of cells as has been described is not in agreement with the comparison and it is regarded as correct that the body is not the sum of similar elementary parts but "an association of structures of unequal importance" (Huek).

If the cell connections turn the body into asyncytial form, that in no way contradicts the existence of the cell state. From the standpoint of the organism cell connection is seen as something very essential and has its significance, but, as we have seen, does not bear on the independence of the cells (Schultze in Schuberg). In the fuller integrity of the organism the relations are not so certain and one can think of the cells in one way, and the whole can be regarded in another way, as organized by a plasmatic vascular system. The body is besides not a giant plasma with amœboid plasma masses wandering through one another, but—due to whatever causes —a cellular structure. This cellulation is the essential thing. Through the plasmatic connections of the cells their individuality and special functions suffer, but the essentials of the comparison are affected as little as separation of men one from another affects the State (Schuberg). The essential thing is precisely their union through intercourse and active combination. It is not necessary to survey the implications of human feeling in an organic growth. What intercourse is in the social organism, cell anastomosis is in the cell aggregate. This might arise as intercellular or as nervous connections.

Also the hypothesis that the organism possesses other living centres beside the cells in the intercellular substance, that it may be therefore an aggregate of cells and of the elements of ground substance, is, if we apply it thoroughly, a hindrance to the maintenance of the comparison. Moreover, the State possesses not only men as physiological units, but art institutions, traditions ; the result of man, of course, but they are no longer man. In a metaphorical sense one can describe this aspect of life as "interhominal substance." Enquiry and discovery, institutions, traditions, new ideas have a life of their own and enter as important factors into the life of the State.

If we use the comparison between the cell state and the human State with some care it would have two effects. The co-operation of the elements of the State rests on quite different assumptions than it does in the organism, and the essence of the State is quite another thing from that of the organism.

One clearly perceives how a conscious activity of the whole is ascribed to man in the State, and so to the cells in the body, and therefore sets up a finalism where there is no preceding causalism. One will therefore deny the formation of the State on a basis of naturalism (formation by the gathering of "hordes") where yet before the formation of the State there has been present the moral striving of the State consciousness in a State builder, his State-forming power, and the education to the State idea starting from him (Grützmacher). Indirectly we may extract the correctness of the comparison from these ideas. It is the teleological adaptation of the organism which has led to the comparison with the State. And if this offers no means for the investigation of the organism it is yet a necessary postulate of the organism ; such, by comparison with the human State, grows extraordinarily impressive and powerful.

(c) The Development of the Multicellular Body.

Para. 104. The (phylogenetic) development of the multicellular body is in no way perfectly clear, and is answered only apparently by the formation of a state in the naturalistic sense. It is not certain that the multicellular animal arises from the single-celled animal. The well known and often illustrated examples are worthy of note in that, for example, the flagellates divide and for a time the products of division remain associated together until the division products separate from one another, and through fusion form a new protozoan (Pandorina). This continues until cells differentiated as ova and spermatozoa are formed (Eudorina). Volvox is generally used as an example of the metazoan, whose cells enclosed in the type of the blastula form six cells that differentiate as ova and spermatozoa. Volvox, however, always remains a protozoan colony, whose cells separate again from one another. Metazoa of the phylogenetic stage of a blastula do not exist (Korschelt), so that Haeckel was the first who presented the gastreæ as the general prototype of the metazoa (p. 320). There is a gap here in the phylogenetic development.

This gap is not bridged over by the " mesozoa," the highest of the simple multicellular animals (haplozoa, lohmanella, orthonectidæ, dycyemidæ (cf. Korschelt p. 140). Some of them produce sexual cells by sprouting. Lohmanella releases from the posterior end a blastula-like vesicle. Rhopalura (orthonectidæ) forms in the larval stage a plasmodium in whose interior the sexual cells develop.

We do not know the historical steps by which the metazoa arrived at the cell colony and there is no need for us to regard the colony formation as the primitive state of the many-celled type. It might probably be the condition of the division of a large plasmodium into cells. As a causal explanation this idea forms a more certain starting point than that only explainable by chance and the supposed greater usefulness of the combining together. Moreover, the cell division of a plasmodial mass is understandable from the physiology of growth in view of the fact that large plasma masses owing to surface tension cannot longer be held together (Lundegardh). From all that we know of the significance of surface tension for metabolism, nutrition and growth, forms of the size of metazoa are not intelligible without cellulation. Also the plasmodial nature of the metazoan body, that is the whole of the cell connections unifying it, would be understandable in this way as primary phylogenetic conditions

(d) Growth, Size of Cells, Cell Accumulation.

Para. 105. We are now brought to problems of the relation of the cells to the growth and size of the body and its organs. The same causes that brought about the first formation of the metazoa must still be at work. Doubtless in cellulation lies the one possibility of the formation of beings of more than microscopic size. Unfortunately we are not yet in a position to demonstrate the laws governing this and so must content ourselves with a view of the more or less valid regulations. The outstanding question is this. Up to what point can the increase in size of the body be referred to the increase of the size of the cells? What limits are set to the increase in the size of the cells? When does cell division take place? Embryonic growth is always certainly bound up with increase in the number of cells until the normal size of the animal and its organs is reached. Then two things may happen. There are organs whose cell number is constant.

In the lower animals this constancy in the number of cells goes so far that there are forms in which the number of cells in the whole body is a constant feature, and within their bodies the organs have not only a constant number of cells, but also the cell groups have a constant topography. Hydatina senta possesses 63 nerve cells, 83 brain cells, 713 body cells. Ascaris possesses a definite number of cells, never one more or less. The position of these cells is constant as well as their form and connections. The same applies to the annelidæ and the gastropods. In the spinal cord of amphioxus and the bony fishes large ganglion cells are found in constant position and number. The fibres of the basilar membrane have a fixed number, as also do the hair cells of the organ of Corti, the cells of the cristæ acusticæ and the maculæ in urodeles, the cells of the retina in vertebrates (Pütter), the lens fibres (Rabl). (For the remainder of the list and figures see Korschelt.)

The richer the organism in cells the more uncertain is such an enumeration and the more difficult the proof of the cell lineage (p. 314). But the probability is such that in the body of higher animals and in man there are organs present with a constant number of cells, and these especially appear in the organs of the animal system (nervous system, sense organs, striated muscle). On the contrary, other organs possess a labille cell number and show cell compensation (skin, connective tissue, supporting tissues, gut epithelium, glands,etc.)

In organs and creatures with a constant cell number growth can only arise from enlargement of the cells. Lower animals of very small size have therefore the largest cells. In animals of different sizes (elephant, mouse) the ganglion cells of the nervous system are constant in number but different in size. Where there is no constant cell number the different size of animals is brought about by the increase in the number of cells, and large animals of the same species have cells of the same size, but different in number. How large the cells of a species become has not been demonstrated. This size is perhaps a species character, and even an individual character about whose mean the size of typical body cells varies.

It is very fundamental that the cell size can be an ordinal, even a class character. All amphibia have much larger cells than the rest of the vertebrates. The urodeles, and among them the phænobranchiates, have the largest cells of all vertebrates (cf. the giant eythrocytes of proteus). Among the fishes the bony fishes are distinguished by their very small cells.

The relationship between the size of the cell nucleus and the cell body has been made responsible for the size of cells (nuclear plasma relation, R. Hertwig, Lubosch). When the size of a cell increases, the surface of the cell body in relation to the mass of the cell for assimilatory processes becomes smaller, and through cell division in proportion to the mass becomes larger. This is doubtless an essential factor, but not the outstanding one, since the nuclear plasma relation can be changed in other ways. It can be altered in a normal fashion through internal relations when other means are available to assist the nutrition of the cell, e.g. the follicle cells for the giant growth of the ovum. It is certain that the nuclear plasma relation determines the time when a cell must divide. It governs the division size of the cell. This, however, depends on the specific size of the cell. How large a cell of a species may become does not depend on the nuclear plasma relation. In respect of the specific size we do not know if the cell size governs the nuclear size or the reverse. The size of the nucleus in itself is no guide, since it is very essential whether the nuclear sap or the chromatin of the nucleus grows, and how the portions of the nucleus are distributed. (For further information on the present state of this question, see Lundegardh. On the nuclear plasma relation, see Lubosch, 1913.)

The number of chromosomes appears to have great influence on the size of the cell. At least one knows that artificial doubling of the chromosomes through hybridization in animals (echinoderms and plants ; œnothera) produces cells double the size and leads to giant growth (œnothera var. gigas). Here again the enlargement of or the diminution of the chromosomes produces pseudogigas or pseudopygmæn (larger or smaller organisms with more or fewer cells, the cell size remaining the same). One ought to admit readily that the constancy of the number of chromosomes and the resulting cell size bear a ratio to each other (number of chromosomes 8, 16, 24—cell-volume 1, 2, 3,) (Tischler). However, this does not explain the reason of the specific cell size. Firstly, the number of chromosomes can be increased in various ways (disappearance of fusion) and it is remarkable that cells which grow with half the number of chromosomes (reduced), as the sexual cells after maturation (haploid), can be as large as the somatic cells with the normal number (diploid). So we recognize many factors determining cell size at any time. However, it has become, through organization, an ancestral promorphological type--race—and individual character as we earlier expressed it [paras. 25, 48, 91].

Para. 106. The increase in the number of cells arises through a process which possesses the widest distribution in animals and plants, and is fundamentally the same in them all: indirect, or karyokinetic or mitotic cell division. The three names describe the most important aspects of the process. Mitosis indicates formation of chromosome threads from a nuclear net, karyokinesis indicates the movements of the nucleus; indirect cell division it is called because cell division is the last act of a series of separate processes, and the special purpose of the whole phenomena is only reached by a long roundabout way (indirect). This purpose is better understood now. The indirect cell division assures to the daughter cells the possession of all the qualities of the mother cell, and in particular the nuclear substance. The maintenance of specific cell size rests on the indirect cell division (quantitative distribution of the nuclear substance) and the maintenance or the alteration of the ancestral specific qualities of the cells, so far as we attribute these to definite qualities of the nuclear substance (qualitatively alike or unlike distribution of the nuclear substance). The mechanical purpose by which this double purpose appears to be reached is this, that the whole of the nuclear substance here coming into consideration firstly from a finely scattered condition collects into extraordinarily long and thin threads, and these threads then divide longitudinally (Roux). Without accepting that the chromosomes have the power to separate, a qualitative halving is brought about by this process, because the errors in the halving of a very large number of parts cancel out (Roux). For reasons we do not know, the thread forms segments, though the essence of the process as described is not changed. All that happens before, during, and after the mitosis, prepares only this one outstanding feature, the longitudinal division of the chromosomes, and from this it again returns to the starting point.

(e) Cell Division and its Problems.

Para. 107. That this process, whose events have often been illustrated and may be taken for granted as known, has not been present in organic nature from the beginning in its perfection is made clear by the many types now known of this unicellular division which are seen as forerunners of true mitoses (cf. full description in Tischler).

Amitosis or direct cell division is that process in which the nucleus and the cell constriction occur without preliminary doubling of the chromosomes. As production of daughter cells " which do not continuously undergo degeneration," amitosis is seldom met with. We can guess that it is present in cells which "at the time" take over purely vegetative functions (for example, the interstitial cells of the genital glands, the transport of fat). Lately the view has been established that the so-called amitosis may be only a subsidiary phenomenon of a nuclear enlargement, which presents on its side a reactive increase of surface area (Benninghof).

The first visible event in the beginning of mitosis is the doubling of the centrosome [para. 113]. This is, however, only the material aspect of the deeper lying dynamic causes of the process which are yet hidden from us. According to all that one knows the disproportion between chromatin and the cell body is at least full of significance for the initiation of the mitosis. The more this disproportion becomes unfavourable to the chromatin, the more the cell body grows, the more the cell system presses towards division. The indication for cell division lies therefore in growth. One can therefore say that growth becomes possible through the individuality of the cell.

Para. 108. The nucleus affords in rest and movement a picture so various that the question of the identity of the forms observed here and there has been disputed and is still unsettled. If in the resting nucleus and in the beginning of cell division (prophase) there is present a sharply stainable nuclear net with nuclear sap in a cell membrane; if at the height of the mitosis (the metaphase) chromosomes markedly stainable, individually formed and constant in number, are present, without nuclear sap and without nuclear membrane in the cytoplasm; if in the final stages there is present (telophase) a new nuclear membrane enclosing the newly formed resting nucleus, and if this change is always repeated, are the questions we would ask. Where and what are the chromosomes in the resting nucleus, and do they in their new formations include portions of the cytoplasm? The first question has been carried further by investigation. The second has gained in understanding by the new colloid chemistry.

The nuclear colloid as distinct from the plasma colloid and separated from it by a membrane (nuclear membrane) undergoes in the process of division a separation (precipitation), (emergence of new nuclear substance, ultra-microscopic, from the nuclear sap, its growth and fusion in solid phases, i.e. chromosomes), and after the completion of division an "intermixture" (the solid phase is formed by transformation of ultra-microscopic particles in the cell sap, secretion of the cell sap wherein the chromosomes alveolize and so again the compact net-like nucleus is established. Resting nucleus and mobile nucleus are therefore the same system whose elements are found in different phases. The resting nucleus, which develops from the division, is accordingly no part of the cell plasma which becomes enclosed by a nuclear membrane, but it is the whole of the alveolized chromosomes (become mixed, net-like).

The origin and the significance of the spindle is obscure. It is admittedly a differentiation of the cytoplasm and stretches backwards and forwards between the centrosomes. One distinguishes in it the central spindle which runs from pole to pole, and the mantle fibres which run only from one pole to the chromosomes. Since the number of mantle fibres and the number of chromosomes in no way agrees, and as also the attachment of the threads to the chromosomes cannot always be proven, it is improbable that the threads exert traction. It is improbable that the spindle fibres pull the chromosomes to the poles, since the necessary changes of form in the spindle cannot be proven.

Attraction and repulsion in electrical fields of different strength have also been suggested, yet there are only hints that any of these may be correct.

The most probable is that there arise in the spindle fibres themselves definitely directed streams of colloid which carry with them the chromosomes. Distinguishable spindle fibres arise, probably first through fixation, whilst in the living dividing cell the achromatic figure appears only in the form of a homogeneous, clear, gelatinous mass, in whose spaces the chromosomes move or are moved (Tischler).[1]

(f) The Chromosome Theory of Inheritance.

Para. 109. Whilst the pattern of the mitosis in all plants and animal organizations is repeated with the greatest uniformity and brings to light the general validity of its purpose, there is one division step which behaves differently. This is the first maturation division of the sexual cells, in which the splitting of the chromosomes drops out and whole chromosomes migrate to the pole of the spindle. Accordingly the daughter cells receive only half the number of chromosomes. The first maturation division is, therefore, described as a reduction division (heterologous, allotypical cell division). The significance of this process is clear, since without it, in each fertilization, the nuclear mass would be doubled, the nuclear plasma relation destroyed, the retention of the typical cell size and accordingly the body size would be impossible. That there is, beside the admitted quantitative reduction, a qualitative reduction present, we can have no doubt. A qualitative reduction is accepted in the chromosome theory of inheritance. This theory assumes that the primordia of the characters exist in the chromosomes; that the reductions and new combinations of the chromosomes may be the material basis of the uniformity of the F_1 generation, and the redistribution, of the characters according to the Mendelian rules and their new chance combinations in the subsequent generations. Hypothetical elements of the theory are the laws of dominance, the parallel combination of the chromosomes, and the exchange of factors according to Morgan (p. 11).

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[1] Most recently (Gurwitsch, Schoukowsky) there have been described "mitogenetic rays," which, starting from a centre, cause mitosis in tissue cells after a definite period, as if the surface of the cells acted as a resonator for the rays. Further effects, which begin in the cells, they believe, are the cause of the special structures observed in the organization centres [paras. 36, 234]. The mitogenetic rays have hitherto been only demonstrated at the apex of the root of the onion. Though generalizations from this should be avoided we cannot omit mention of these mitogenetic rays.

(1) *The Theoretical Implications.*—Differing from the mitoses of the body cells, the young oöcytes and spermiocytes, after the last oögonia and spermatogonia division of the nucleus, enter on a long resting stage, during which the chromosomes are only present in a state of finest subdivision. After thickening, the chromosomes first again arise as fine threads in order to fuse into a dense ball of chromatin (synapsis). This ball loosens and so there arise, without exception, pairs of chromosomes and consequently half as many pairs as there were chromosomes. The threads of these pairs are wound round one another in a complicated fashion. The division which they enter is the primary division. After passing through a second division (the secondary division) each individual thread can be divided again lengthwise, or this may be deferred till later. So, instead of each pair of chromosomes entering the synapsis, four elements leave it, which together form a tetrad. The total number of tetrads is, therefore, the same as half the chromosomes (out of the two chromosomes a and b comes a single tetrad. $\dfrac{\frac{a}{a}}{\frac{b}{b}}$.) After the formation of the tetrad the first step of division brings about a separation of the elements along the primary split. This perfects the reduction. There is separated $\frac{a}{a}$ from $\frac{b}{b}$. The second maturation division runs then according to the usual type, a separates from a, b from b, through

the secondary division. Altogether we had n chromosomes in the whole, $\frac{n}{2}$ tetrads, then $\frac{n}{2}$ dyads after the first, $\frac{n}{2}$ chromosomes after the second maturation division.

Therefore the fact is fundamental and well established that every organism is a double (diplont) being in its nuclear form (anatomically and genotypically), though it behaves as one according to appearances (phænotypically), and in relation to inheritance (Johannsen, p. 479). First through the formation of ripe sexual cells (spermatids and ripe eggs, "gametes") every organism is again transformed into a single being (haploid). The double structure of the diplont rests on fertilization. The chromosomes spring half from the father and half from the mother.

(2) The hyothetical elements of the chromosome theory:—

(*a*) The paternal and the maternal chromosomes present a perfect apparatus of inheritance; in each diplont there are virtually the hereditary factors of two beings present. Each chromosome includes a part of the hereditary factors (an id, Weismann). Two ids are homologous (a paternal and a maternal). The smallest visible elements (chromioles) included in the hereditary complex in homologous ids have the same special position, the same special distance from one another (Morgan).

(*b*) In the synaptic parallel conjugation the homologous chromosomes are parallel with one another. A mutual exchange of homologous groups, in a block-like fashion, can take place. Genotypical change (mutation) arises in the distribution of an id. The new hereditary factor has not the homologous partner (absent or present).

(*c*) The reduction gets rid of a complete set of primordial factors not in order that the original threads may separate from one another, but so that the new haplont thread may include ids of both threads.

(*d*) The junction of the two haplonts brings about the new diplont (F_1).

(*e*) That the diplont, of course of double structure, is phænotypically single is the result of the rule of dominance in the heterozygotic fusion.

By all this the phenomena of Mendelian inheritance would be explained, though here we cannot go into this further. The abundance of the possible combinations is clearly unlimited. In general each organism will furnish as many Mendelian characters as it has ids in the haplont condition. A being with 24 chromosomes[1] in the diplont state (man) forms 2^{12} sorts of sperm and 2^{12} sorts of ova. When fertilization occurs there are 2^{24} new diplonts possible.

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[1] Lately 48 chromosomes in the diplont condition for females and 47 or 48 for males is the estimate.

Therefore the possible new combinations through the exchange of factors is unlimited.

On some fundamental difficulties of the whole theory, cf. para. 115. On conjugation, not lengthwise but endwise, cf. Morgan and Tischler.

(g) Age, Death of the Cells.

Para. 110. Questions of the length of life of the cells, and accordingly of the length of life, age and death of the organism, are closely related to the propagation of the cells and the development of the organism. The length of the life of an organism, so extraordinarily different (animals and plants, see the extensive lists in Korschelt), is yet obscure in its basis. We do not know if it depends on the size of the body, or upon the length of the embryonic development, or on the intensity of metabolism, or anything else. We find ourselves in the same state of ignorance in regard to the survival of species of which a few have persisted from the earliest times unchanged, while most progress and after a longer space of time disappear. In respect of the individual we only know that their survival depends on the co-operation of two factors: on the resistance capacity which diminishes during life, and on the injurious influences externally which remain the same during life (Pütter). Age consists in the diminution of the resistance factor.

This resistance factor and its diminution is a phenomenon of life. However, as the life of a person and the life of a cell is the same life, so also the age of a person is the age of the cell, and the death of a person is the death of a cell.

Both do not happen together. There is old age of cells in young bodies without death of the person, and death of the person without death of all the cells. It is known that in death of the person many cells live longer. Organs (heart) can continue long to function. One takes bits of tissue and cultivates them outside the body so they can yet live, whilst the animal from which they were taken is long since dead (Korschelt, p. 243). Consequently the cells show their existence as a life group, since the death of the person, as may be shown, is under all circumstances a cell death. The transformations concerning age and death are accordingly linked with cellular processes.

The old teaching of the potential immortality of the unicellular being is known. Since it divides and in the products of this division continues to live, it appears immortal. The fact that the sexual cells of metazoa, in so far as they succeed in propagating, continue to live in the cell stem which provides again the sexual cells, led, first

A. Rauber and, after him, Weismann, to the conception of an immortal germ plasm which the mortal body tissues carried from sex to sex. In this conception there is much truth. The theory of heredity, as we now possess it, applies it in the theory of the continuity of the gene.

However, in this later modification there comes a correction of the older view of the immortality of the unicellular organism. As the whole of the sexual cell does not survive, but only that part of it which carries the material of heredity, whilst part of the body obviously degenerates (tail of the sperm, Schleip), or is used up in the course of development, so the unicellular organism is only immortal in respect to its heredity element (gene). As an individual it dies completely, since it gives its individuality to its two daughter cells (individual death without the presence of a body, Kraus). Under all circumstances, apart from this, it suffers a partial death (Doflein) since part of its body (macronucleus) regularly degenerates.

Individual death, partial death, partial immortality, are therefore joined in the unicellular animal in one and the same individual. In the metazoa there is no difference. The new thing that arises is the body. If one ignores the corpseless individual death of the unicellular organism, then personal death (physiological death), the formation of the corpse, is the consequence of organization affecting only the metazoa. Partial immortality is enjoyed by the gene in the metazoa. The unnumbered body cells suffer partial death right from the beginning of embryonic development, at all times in post-embryonic life (red blood-corpuscles, zymogen granules, gland cells, epidermis cells). It is the same in organs and derivatives of organs (gills, gill slits, chorda, thymus, mammary gland, hair, nails, teeth). The destruction is often the necessary precursor of development (metamorphosis of insects, ossification, our entire skeleton is formed anew on ruins).

All these partial deaths do not affect the life of the person. Its physiological death first arises with the formation of the corpse, when the partial death affects such cells and organs, without which the life of the whole organism cannot go on, if these cells and organs find no compensation. The view has been put forward that many body cells may be compensated indefinitely, that therefore, for example, the cylindrical cells of the deeper layers of the epidermis, like the sexual cells, are potentially immortal. Death, however, comes to them, since in consequence of the organization of metazoa this immortality of part of its elements cannot come to expression, and because the other part which has lost the capacity for unlimited increase, "plunges the others into the catastrophe with it" (Rössle). Physiological death depends therefore on the fact that there are in the body cells of more importance to life, which cannot be compensated. In thus far death depends on the constancy of the number of cells, that is, above all, on the formation of the animal systems.

Age depends on the death of these and other more replaceable cells. We know unfortunately only the gross aspects of age which can arise in all organs and tissues.

In epithelial organs may be mentioned the opacity of lens fibres, and the conjunctiva (grey arcade), the atrophy of the tooth enamel, greying and falling out of hair; in organs of the supporting tissues, the relaxation of elastic tissue, and the over-extension of connective tissue (age sinking of organs), the changes in the intima of blood-vessels, the atrophy of bone, the falling out of teeth, in the muscle tissues, the calcification of the muscular coat of arteries.

What are the cytological phenomena of age is yet little known; at best in the nerve cells, whose Nissl granules are changed whilst at the same time a granular age pigment appears (lipofuscin). This pigment is also found in the muscle cells of the heart and the crossed striped fibres, particularly of the respiratory muscles. Lately the view has gained in favour that changes in the colloidal form of the cell protoplasm may be the spontaneous cause of ageing (hysteresis of the cells, which would diminish the capacity of the cell for self renewal p. 386.) However this may be, it is certain that it is the life process itself through which the cells pass to old age and finally to death as soon as the power of regeneration becomes too feeble to repair the injurious effects of metabolism on the living substance of the cell.

This repair belongs to the phenomena of rejuvenation, and of course we call it spontaneous in opposition to artificial rejuvenation. As rejuvenation in the strictest sense would be described the "shedding of complicated forms," return to simpler proportions, and the regeneration of parts from these as does arise at least partially in unicellular animals (Korschelt, p. 258) during conjugation. This applied to the cells of metazoa would signify "dedifferentiation" (p. 315).

If we ignore perfect dedifferentiation, then we can regard as rejuvenation in the adult body, repeated differentiation, backward differentiation and foward differentiation, as such. So far as division of the cells occurs at the same time, then cell division is a means of rejuvenation. Continuous division hinders differentiation and therefore frees the cells from their products of differentiation and delays the onset of cell death (Weidenreich). Also the investigations of Peters have taught us that only during periods of cell rest are the functions of the cell fully used. During division the functions of the cells are in abeyance. It can also be shown experimentally that the functions of a cell are more energetic and powerful after cell division than later (cf. in Korschelt). (On the effects of hormones and artificial rejuvenation, cf. Harms, Steinach in Korschelt, Chap. XIV.)

In summary we may say that age and physiological (age) death are a function of the life of metazoa, that death necessarily develops from life, and that organisms necessarily die (necrobiosis). In a final sense death *must* arise, since higher differentiation and the specific function of definite cells are only possible when they lose their capacity for increase. Here lies the necessity of death. So the development of the whole complicated organism and the differentiation of its highest levels particularly, in its psychical qualities, may be regarded as the cause or consequence—as you will—of physiological death.

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(2) The Cell as an Elementary Organism.

(a) Cell and Cells.

Para. 111. All the descriptions of cells in most textbooks and monographs of earlier times included a simple figure—one circle with a smaller circle lying eccentrically within it. Now we strive to figure the cell as a paradigm, and of course using neither the simplest possible (a red blood-cell) nor the most complicated (the ovum). Here the general difficulty is brought out of which the beginner is not generally conscious, in that there is not "a cell" but only cells. The intellectual abstraction plays here as elsewhere an important rôle; unusually so, in that it is more important here than in the systems generally (p. 92). Cytology signifies therefore the representation of the features that must arise in every cell, leaving out what is specific in the structure of individual cells. If one goes through the characteristics of ova, spermatozoa, tendon-, cartilage-, ganglion-, etc., cells, one grasps the value of the conception by which it was recognized for the first time that in all cells there lies some general quality (Schwann).

Admittedly this general quality, as the name "cell" implies, was in the beginning thought to be features other than those actually met with, and historically (M. Heidenhain) our more recent cell conception contains two different ideas. The older, which saw as the essential the cell boundary (cellula), considering the contents as only the matrix of the wall (Schleiden), and a younger which saw the essentials precisely in the contents (sarcode, protoplasm), and saw in the nucleus not only the crystallization point of a new cell, but a persistent cell organ (Remak, Kölliker, and especially Max Schultze). Out of this there arises the definition of a "cell" as a spatially limited mass of protoplasm containing a nucleus (Max Schultze).

This definition is pure morphology; it is applicable to all cells exactly as species and orders may be defined. The science of cells is deepened and extended if the morphological definition be joined to a genetic and a physiological one in which one would recognize as wrong the acceptance of the free establishment of this protoplasmic mass (rather omnis cellula e cellula, R. Virchow, p. 33), and in which one would learn to see the morphological spatial limitation actually as the expression of an individuality. Accordingly the cells first become the elementary bearers of life (elementary organisms, Brücke). Partly following a new definition (Heidenhain) we will define the cell thus: As an element spatially limited arising from protoplasm, differentiated into body and nucleus, which behaves morphologically and physiologically as an individual, and is derived only from older cells. The last clause is probably to be taken to mean that the nucleus also is derived only from older nuclei or nuclear substance.

The division of the cell into protoplasm and nucleus, repeated in most descriptions, we regard as useless, since the opposite to nucleus is the body; the whole cell body does not arise from protoplasm and also the nucleus arises from protoplasm, only one describes this part as karyoplasm. The meaning of the word protoplasm (primitive material) is best given in the expression "living substance," which, as a constituent of the cell, therefore morphologically included, is admissible. The nucleus is formed wholly of living substance, the cell body on the contrary contains within the protoplasm numerous inclusions certainly which do not look like living things, and which one classifies as deuteroplasm.

The differentiation of the cells we need to consider fully under the form of a division of labour in so far as the cell body stands in intimate relation with the outside world, and serves metabolism, the stimulus conduction and the movement phenomena, whilst the nucleus, the more withdrawn part of the living substance, includes the continuous cycle of the cell lineage. It would be permissible to believe that the nucleus contains the visible structures and materials that bear the inheritance, that at all events if there are present in the cell body bearers of inheritance those localized in the nucleus would need to have to fill some other purpose. Ignoring the special significance of both parts of the cell, it is certain that exchange of work arises between both of a sort that neither an enucleated cell (also no enucleated experimentally separated fragment of the cell body) nor a cell-free, perfectly isolated nucleus can continue to survive. The latter is understandable because the nutrition of the nucleus is dependent on the cell body; the former depends accordingly on the fact that from the nucleus there issues a regulation of the life processes of the cell. What manner of regulation this is we do not yet know (energetic, chemical (ferment) or both).

(b) The Cell Body.

Para. 112. In respect to the structure of protoplasm it is usually stated that four different theories of the nature of protoplasm have been derived from the older cytology: the thread theory (Flemming), the net theory (Frommann), the alveolar theory (Bütschli), and the granular theory (Altmann). The differences between these may be striking.

The teaching that protoplasm may be constructed according to a single one of these four types is not to be maintained. Moreover, thread-like, alveolar, and granular forms arise in different cells beside one another, and in the same cell at different times after one another. They are functional structures in which the living activities of the cell are made known. Only do the granules, as the latest visible structural element, bear a special significance. Before all it has been shown that the threads, like the alveolar wall, and even the alveolar content, are derived from granules. In this sense the granules have been described as plastosomes, the threads arising from them as plastoconts (chondriomites). These thread granules, originally found in the sperm, have been demonstrated as constituents of all animal cells. This is quite the most important advance which cytology has made in the last ten years (contributed especially by Benda, Mewes, Duesberg, O. Schultze).

The plastosomes are found everywhere in the cell body, they form the threads of the filar mass, the walls of the alveoli, and join together the sharp, clearly movable plasma masses of the hyaloplasm. They lie as an extensive mass in the sarcoplasm of the muscle cells and muscle fibres, in the nerve cells the same, especially in those of the brain cortex, and exhibit in isolated cells when dying the phenomenon of Brownian movement (molecular). They are formed of the finest granules joined in a most complicated fashion (O. Schultze). Their physiological significance rests above all on the fact that they are the visible expression of the form and tendencies of the metabolism in cells (O. Schultze). It can be shown in connective tissue that the fibrillæ arise in the exoplasm by the fusion of the granules. They arise in the same way in muscle and nerve fibrils. Plastosomes are used in gland cells for the formation of secretion. They form large granules which are in turn developed from invisible particles. On and in them, fat (fat granules) and pigment (pigment granules) accumulate. Also the accumulation of absorbed substances is bound up with their existence.

Especially important for the study of these absorption phenomena have been the results obtained by staining the living cells (vital staining). This was first carried out by O. Schultze. Through these investigations a glimpse of the transport of substances within the tissues and their physiological acceptance by the cell has been obtained (v. Mollendorf). Also here it has been found that the vital dye has been accumulated in definite granules.

From a genetic view the significance of the granules as the elementary bearers of function is possible in that the ovum as the least differentiated elementary organism exhibits the granules in less complicated form, even as very fine granules. In the later sexual cells of the organism the granular form is retained (plastosomes) whilst in the tissue cells they fuse and form threads and rods (Mewes, Rubaschkin). So the whole type and trend of metabolism of the cell is bound up with the presence of particles which on their part arise either individually or as specifically different stems (?) from the general mass of the protoplasmic living substance. Since the smallest visible granules with a size of 1μ lie at the limits of visibility (para. 100), their emergence from the living substance remains invisible at present. In no case are they elementary organisms in the sense of Altmann, or are the cells a colony of such. That would take their constancy and individuality for granted. They show, however, a coming and a going, they grow, become either sacrificed (secretory granules) or preserved, and differentiate into other forms (fibrillæ) after a longer period. In fewer cases the granules have shown like the cells themselves a constant number (Vonwiller); and of course in the lowest animals (plasmodium of the myxomycetes) where they singly always appear regular. A part of the granule plays a special rôle, perhaps, of which in individual cases it has been proven that it has become equally distributed to the two daughter cells in cell division (Mewes, Held). A part of the inherited qualities are in all probability bound to these granules. What this is and how far it is distinguishable from the nuclear inheritance we do not yet know. The heritable individual specificities of the plasmatypes, fibrillæ, etc., and accordingly the constitutional condition so functionally various in inheritance (e.g., the inherited weakness of the connective tissue fibrils) may be perhaps referable to the plastoconts. It is known that embryonic development reaches right up to the gastrula stage without the intervention of the nucleus on the cell, whilst at this time certainly, probably also later, cytoplasmic influences are effective on the constitution of the cell (cf. in Penners).

Para. 113. The interior of the cell body includes a different cell organ, the group of central bodies or centrioles. This group arises with the differentiation of the protoplasm. The central body forms the central apparatus as well as the surrounding plasma masses.

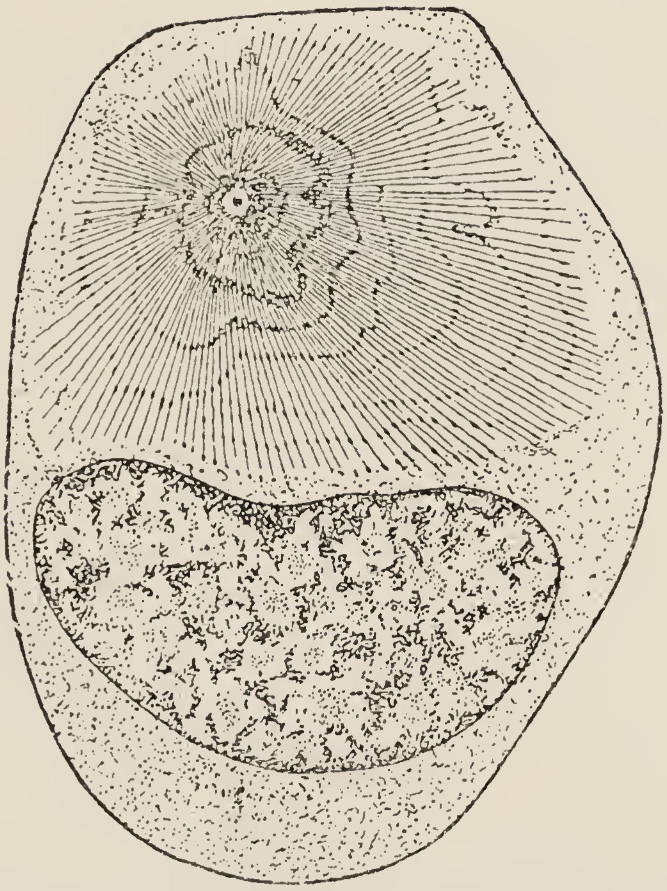

Fig. 65. Spermatogonium of a salamander, after Drüner. Appearance of the concentric rings of the sphere. From M. Heidenhain. Plasma and cell, fig. 155.

At most there are several centrioles (2-3) and they appear as homogeneous granules which in size are $0{\cdot}8\mu$ to $0{\cdot}2\mu$, and therefore lie at the limits of visibility. Their finer form therefore cannot be resolved any further by the microscope (para. 100). They are to be described as histomeres of the first degree (Heidenhain). The investment (centrosome) is a vacuolated plasma which is surrounded by plasma rays (sphere) at certain times (division) in the life of the cell. This sphere whose rays are radii of a circle can be arranged in the most complicated circular pattern (on the average zone-like). (Fig. 65.)

For the appreciation of the significance of the central body it is worthy of note that it is absent from plant cells. It is only a necessary organ in animal cells. In these it has, as an essential morphological special organ, the sphere apparatus which occupies a definite topographical position in the cell (Heidenhain).

In round or flat cells the central bodies lie chiefly so that the connection between them, the middle of the nucleus, and the middle of the cell, forms a straight line (fig. 66). In cylindrical cells the central body lies underneath the free surface, the connection between them goes through the middle of the cell and is perpendicular to the free surface.

This constant orientation of the cell parts around a structural axis appears to us to be of very great importance for our ideas of the promorphology of the cells [para. 97] although it is something other than the stereometric axis of the cell. In what relationship these two axes stand to each other and what importance each of them possesses for the structure of a typical cell is not yet explained. The existence of the centriole probably serves to maintain the constant spatial orientation of all cell parts to one another. Especially is it true that the outer investment of the animal cell does not limit its capacity to change its form. This makes a contracting centre necessary in contradistinction to plant cells enclosed by a firm wall. By what means the central body exerts this directing influence on the cell is at the moment unknown.

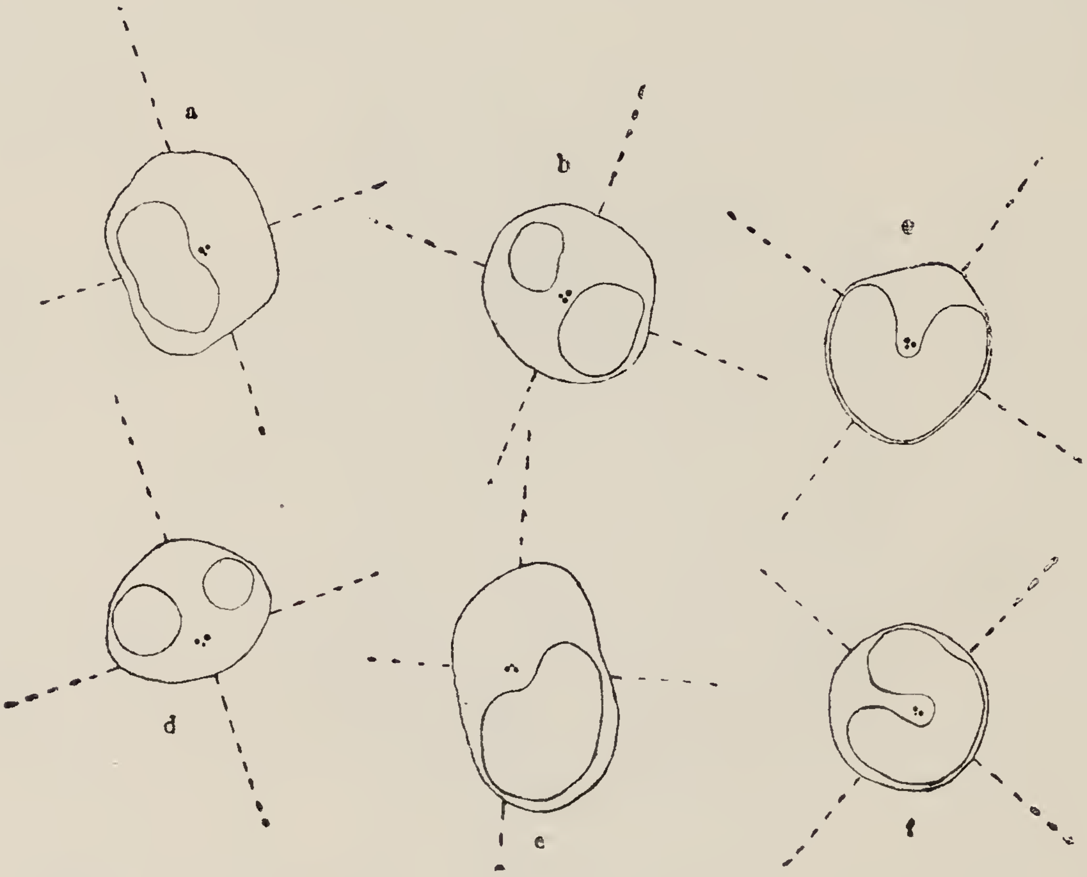

Fig. 66.—White blood-corpuscles from the bone-marrow of the rabbit. Position of the centrioles. The middle of the cell, the middle of the nucleus, and the centriole lie on a straight line (structural axis of the cell). From M. Heidenhain, Plasma and Cell, vol. i., fig. 131.

For the sake of illustration and as a metaphor for the form of the sphere rays, we may perhaps think of a magnetic or an electrically active centre. Yet on the basis of known observations it is better to regard these rays as directive streams which run from the periphery to the centre.

Also the rôle of the central apparatus in cell division upholds this conclusion. That the central body (first the central body, then the sheath) introduces each cell division is not to be explained unless in the central apparatus there is a "kinetic centre," for plant cells too divide and cell division can be artificially excited. Also in fertilization induced by the entry of the sperm in the ripe egg, the rôle of the centrosome and of the central body is not exclusively that of a development-regulating mechanism since development can also be artificially excited.

The significance of the central apparatus as a centre for the maintenance of a firm cell structure would explain why each division necessitates an orientating centre for the daughter cells, and why these centres are the first to divide, and why the wandering of the daughter centres to the poles of the spindle satisfies this necessity.

(c) The Nucleus.

(i) At Rest.

Para. 114. The following conceptions of the structure of the nucleus have recently been formed; in the resting tissue cells it is perfectly separated from the cell body by a semi-permeable membrane. Its interior possesses a coarse web-like structure. The walls of these web-like spaces are of stouter material, which again presents a web-like structure. In this way is formed a firmly-bound scaffolding (nuclear scaffolding). The substance out of which this scaffolding arises is described as linin (plastin). A clearer, more mobile substance forms the content of the alveoli, which is termed nuclear sap (nuclear lymph, karyoplasm). The nuclear granules are a second formed element of the nucleus. These are called chromioles. They cannot be assigned to either of these two elements, since they lie in the nuclear sap, and also help to form the tougher of the nuclear threads, so one must regard the nucleus as an aggregate of the finest granules which lie partly in the scaffolding and partly in the nuclear lymph. The whole mass of nucleus whose parts can be transformed into one another under different conditions is therefore something of a unity though functionally subdivided, which, following the botanists, can be described also as karyotin. The chromioles resemble the centrioles in regard to size. They therefore cannot be resolved any further optically into elementary parts (Heidenhain).

The nuclei only exhibit these forms when specially treated. Usually, especially in the preparations available to students, they are made visible by being stained in the dead cells with dyes (so-called basic or nuclear stains). The scaffolding appears only more or less darkly stained, since such stains make clear only the chromioles lying in the scaffolding and only a part of these, so that the nucleus appears traversed by a " chromatin " network which is permeated by the non-stained nuclear sap. The stainable substance of the nucleus, from this peculiarity of staining with basic dyes, receives the name of chromatin. In the resting state most of the nucleus appears stained compactly under our best microscopic systems, since the alveolar spaces are very small and are covered over by chromatin threads lying in other planes. Only large nuclei (gland cells, nerve cells, sex cells) show the network more clearly.

This staining of definite nuclear substances rests firstly on the chemical affinities which they possess for definite dyes, secondly on the stage of division and the thickness of the nuclear substance [para. 100]. These nuclear materials are distinguished from the substances of the protoplasm of the cell body by the presence of phosphorus, which is present in the nucleic acid. This is always in combination with protein, so that the nuclear material may be regarded as a protein salt of nucleic acid (nucleoproteid). The amount of nucleic acid in the nuclear substance varies with the sort of nucleus in different tissues and in the same nucleus at different periods of activity. So one distinguishes different sorts of granules, basophile and oxyphile (basi- and oxychromatin) ; the linin net is also oxyphile.

This dependence of the staining on the distribution of the phosphorus-containing elements in the molecule is therefore not a purely chemical but also a physical factor. Not the chemistry alone, but also the mass of the phosphorus-containing groups in the molecule determines the staining. Therefore it further follows that the different chromatin types do not differ chemically or in their essence from one another, and that chromatin is not a chemical but a micro-anatomical conception (cytomorphological).

The phosphorus-containing nucleic acid is found not only in the nucleus. Chromatin substances are also found in the cell body. Despite this we need to describe it as a substance arising in the nucleus for preference, which therefore has something to do with what has been described hypothetically as a " gene."

From a more functional view chromatin is divided into idiochromatin (the essential substance especially subserving inheritance) and trophochromatin (which subserves the metabolism and the nutrition of the idiochromatin).

(ii) Nucleus in Activity.

Para. 115. This is distinguished from the resting nucleus in special ways and of course morphologically. The net draws in first its fine bridging threads, then arises next a looser, then a thicker skein. This separates into chromosomes, the number being constant for the species, though differing in size and form. The nuclear membrane disappears. Then chemically the oxychromatin dwindles and is transformed completely into the basi-chromatin condition. The young chromosomes are first V-shaped, then they flatten and become shorter and broader. The longitudinal splitting is often exhibited long before the stage of the equatorial plate, often just when the daughter nuclei have formed. Since the longitudinal splitting shows that the chromosomes have finished growing, it follows that the maximum point of growth of the chromosomes is reached before the beginning of the next cell division. This division, as already stated, is produced through the cell growth following the growth of the chromosomes and through the tension arising between the cell and the size of the nucleus [para. 107]. Since usually after all divisions following one another in the same cell system, the chromosomes recur in the same number, size and position always, three questions have aroused the interest of cytologists. These, as is easily seen, penetrate into the most intimate nature of things and impinge on the most profound problems of form formation. They are: (1) Where are the chromosomes when the nucleus is at rest? (2) How do they arise from the chromatin net? (3) What is the fine structure of the chromosomes, are they some solid morphological preformation?

The first question is absolutely obscure. We can only say, having regard for the opinion of Heidenhain: An organization must be present in the resting nucleus, out of which of necessity arises the constancy of the chromosome number, their form, and their relation to one another. Heidenhain has asserted his view that the linin groundwork determines the constancy and form of the nucleus. To this linin territory he ascribes the capacity of true contractility, in order to explain the shortening and the thickening of the chromosomes. This might be explained also in quite other ways (p. 362).

In respect to the second question, what has already been said in regard to colloid chemistry on the processes of the formation of chromosomes plays a part. Here the relations of the chromioles to the chromosomes comes in. The opinion has been formed that within the nuclear net there are present morphologically distinct areas; within such an area in the transformation of the resting nucleus into the dividing nucleus the thickening and the streaming together of the chromioles take place. One chromosome corresponds to one such area. These opinions were first enunciated by Rabl on the form and arrangement of the chromosomes, then by Boveri on the special peculiarities of the dividing cells of Ascaris. Through a number of special investigations, the same phenomena which arise during the maturation of the ovum and the sperm have more and more been shown to be correct. The hypothetical areas are the tactical points for the troops. The chromioles are their special troops which distribute themselves according to plan, can be collected and grouped for other manœuvres in other formations (the manœuvre hypothesis of Fick). The chromosomes are only tactical units. After completion of the division a chromosome is transformed again into its territory of the resting nucleus.

The third question, the fine structure of the chromosome, is now generally answered by a comparison between the chromosomes and a string of beads. It is suggested that the chromatin granules on a linin basis are strung like beads on a thread. It has been well observed that a striking morphological regularity predominates. The series of the chromosomes, differing in size, of a nucleus show the threaded chromatin granules of different size within each individual chromosome and the interval between two such granules is of different length. One must need conclude that within the species not only the number of chromosomes may be constant but each individual chromosome possesses a typical morphological structure (Morgan). This leads to the next point, that in these granules the genes are either localized bodily or in them at least the state of their activity must lie (fermentative).

Such a hypothetical morphological basis the American school of geneticists (Morgan) after long and careful hybridization experiments has framed on the four haploid chromosomes of the sexual cells of Drosophila. They have achieved the construction of chromosome charts with a fixed position of the character equivalents. (Morgan for Drosophila, further examples in Tischler.) These demonstrations are still at this moment the subject of criticism. Moreover, the two fundamental presentations of the finer structure of the nucleus of animal (Heidenhain) and plant cells (Tischler) in a valuation of the whole material reckon all the angular appearances of the chromosomes as artefacts, and regard only perfectly smooth chromosomes as representing the natural condition. The newer investigations criticize these statements.

It is certain in each case that in the resting nucleus the chromioles do not remain intact and unchanged in their areas. Active metabolic processes and shifting of position occur. It is certain that they undergo in part transformation and renewal so that the chromosomes arising in the region of the resting nucleus, which in a gross view must be regarded as identical, are certainly not materially identical in respect to their finer structure.

(iii) Chromosomes ("Genomes") and the Formation of Species.

Para. 116. Here now we must proceed with quite special care, for cautious consideration will at once make it clear that in the last resort the changeability of form, species formation, which, as we learnt above [para. 32 G] is the source of transformation, is with difficulty reconciled with the unchangeability of the chromosomes. We have numerous approaches now for the appreciation of this relation from whose perfect explanation we are still very far distant.

In a descriptive view the different sizes and forms of the chromosome groups of a species are very remarkable. If, for example, there are 1-4 chromosomes, then in all the body cells chromosome 1 agrees with 1 and likewise 2, 3 and 4 (the whole group is then the "genom"). Comparing different races of the same species one often observes differences of identical chromosomes in respect to their size and form (e.g., in the chromosome number 1). In the comparison of different species such differences are present in marked degree. They can go as far as the degeneration of a chromosome into a small fragment, even to its disappearance, so that the chromosome number within a species of a genus exhibits a typical diminution. An extensive survey on the number of chromosomes in the classes, orders, species, varieties of plants, the reader will find in Tischler; besides numerous estimates for animals (cf. also chapter, Species, and the Maturation of the Ovum, in Lubosch, 1913). On the other hand, experiment has shown that changes in the state of the genom (increase and diminution) influence hereditarily the developing organism (giant or dwarf forms, p. 359). Also increase or diminution of a particular chromosome experimentally produced leads to changes of body size.

So there arises quite certainly a relation between the genoms and the form of the organism and between the unfolding of one and the other.

We can only follow those changes which are of a quantitative kind in the genoms at the moment. However, in view of the whole position, it can scarcely be doubted that there are qualitative changes of the chromosomes which must have a pronounced effect on the unfolding of form. This would be the unfolding of the G of the reaction formula to a G_1 [para. 32]; how and under what conditions this follows cannot be stated at this moment. "In itself," the process appears so little like any other organic process. Since the nucleus stands in such intimate relation with the plasma, nutritive influences in the widest sense, as Weismann already implied in his theory, must be made answerable for this, as well as crossing over with the ensuing changes in the inner constitution of the chromosomes.

Still more difficult is it to answer the question "when." The most likely idea is that there may be a time when the germ cells within the body are open to somatic influences. The time of the growth of the ovum and its maturation have long been regarded as periods of finely divided chromatin and therefore of account (Lubosch 1902).

It has been shown since, experimentally, that this period is indeed a "sensitive period" in the sense that during it the germ cells can be influenced by exogenous events hereditarily. (Standfuss and Fischer in butterflies, and Tower in the Colorado cockchafer.) Under parallel induction (Detto) one understands the process by which a stimulus works on the body and the germ cells at the same time whilst most recently it has been shown by Stieve that also through stimuli, which only work on the body, the germ cells may be affected harmfully along with the body. Naturally it has not been proven that these changes of the germ cells are at the same time a change of their constitution, yet they do show a way in which such changes may arise. The connection with the above problems [para. 34], in particular to the conception of an unfolding of the germ-plasm following orthogenetically under the influence of stimuli, is given here.

In particular after all we now know on structure, form, and form formation and the inner constitution of the chromosomes we are correct at this time in distinguishing sharply between these forms and the hypothetical form of the germ plasma. The chromosome itself, whose capacity for change occurs not only in different phases of cell life, but also in the development of the species, cannot be the final element in the formative processes. It is itself only a "phenomenon," a "momentary form" (Fick), at every moment governed by constitutional and functional factors of the whole condition of the nucleus.

A water turbine arranged for the watering of garden-beds is an intelligible example of how a large structure can be only a momentary form of what apparently works on a complex combination of structure and movement. If one looks from a distance at the water stream of the apparatus it appears as a constant structure (chromosomes) and yet its form depends on the form and number of the turbine arms and on the speed of rotation, the direction, width, and number of outflow openings and finally on the supply of water. In the cell we know at this time nothing of all these factors.

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(B) Leptonomorphology.

(1) The Colloidal Structure of Protoplasm and its Importance in the Morphology of the Cell.

Para. 117. In this whole presentation our object has been to present anatomy as the science of form. From the largest to the smallest we find differences of form, but always form. Also in the cells we find form and size relationships classifiable stereometrically. Behind the chromosomes themselves there stands something building and retaining form. Between this and the pattern of the whole we see relationships. What type they might be we cannot say at this moment. We must take for granted that the cell structures, known to us now, are the expression of other forms of the living substance yet to be revealed. Crystallography has invented (Rinne) the expression leptonology for the science of finer form; we can take this over for the science of the finer structure of living things. What conceptions can we now make of this finer form? It is taken for granted that we must accept in living substance not only the possibility of regulated formative processes, but also that they can be proven in some degree. The question whether the living substance may be a solid or a fluid aggregate has so long been before us that it is difficult to form an opinion on this. This controversy, now only of historical interest, always ended in the insoluble contradiction that protoplasm was to all appearances not solid, while, however, if we ascribe to it a fluid aggregated condition, the hereditary persistence of form-retaining and form-forming factors is no longer understandable. The recognition that the difference between solid and fluid is only a difference of degree, and that the colloid state stands intermediate between both, has essentially settled this contradiction.

All organic material now appears to us as a reversible penetration of two substances, of which one is so dispersed in the other that between the particles of the one and those of the other there arise separation surfaces (disperse system). Both the substances of such a system are described by the peculiar expression, which has quite another meaning, "phases." This phase in itself can be solid, liquid, and gaseous, so that a system of complex combinations can arise. They all fall under the name of "solution" wherein the solution medium (dispersant, dispersing phase) stands opposite to the dissolved substance (dispersum, disperse phase). Of all possible combinations, the suspensions (solid in fluid) and emulsions (fluid in fluid) are the most important for us since between them stands the colloidal solution according to which type the organic body is fashioned physically. Whilst in the suspensions the distribution of the dispersum is made in quite large elements so that they remain visible (droplets), they grade into the colloidal solutions so far that particles of submicroscopic size arise (transitions, suspensoid colloid) until they can be compared to molecules (emulsion colloid). If the dispersion continues right up to the molecular stage then we get true solutions.

The colloids coming into consideration for the aggregate state of protoplasm are the emulsion colloids, which in many characters show their near relation to true solutions. The most important of the general features is that the dissolved phase, if it becomes concentrated by dehydration, can always take up water again. It can always return to its starting point. Emulsion colloids are, like true solutions, reversible (hydrophile). This reversibility of water-acceptance and water-loss is an indispensable condition for the maintenance of life.

If the dispersum is dissolved, there arises a sol (sol-ution) within the solution medium, in nature mostly water, therefore hydrosol (-ution). From this solution it can be separated by coagulation, precipitation, etc., and be brought into a more solid state. It may then be a jelly, and the system falls into a dispersant and gel. The form of a colloid disperse system is complicated, because each phase can be again formed as colloidal (complex colloidal solution), as it certainly is in protoplasm, in a very complex form.

Of the morphologically finer forms the ultramicroscope provides a glimpse. This rests on the principle that if dissolved substances become illuminated laterally through a sharp cone of light, and this illuminated field of the fluid is viewed through a microscope, we can observe them in the same manner as we see the dust in a sunbeam in a darkened room with the naked eye. The dark-ground illumination effected through a special condenser on an unstained object works similarly. What are here visible in the microscope are not the individual disperse particles, since their distances from one another are smaller than 0·2 μ [cf. para. 100]. However, we see the displacement of the cone of light starting from the particles themselves which have become illuminated. The difference between the picture granted by a glimpse through an ultramicroscope and that given by a microscope is that in the microscope particles are seen according to their form, while in the other only an optical proof of their presence is obtained, without any resemblance to their form. The above [para. 100] mentioned limits of optical resolution of particles is, therefore, not as such an optical proof of particles. Mass particles of very much smaller size than half the wave length of light are optically provable. Therefore, one measures the ultramicroscopic elements not by "μ," but by double-μ "$\mu\mu$" in which a $\mu = 1{,}000$ $\mu\mu$. In general, the following divisions of size apply :—

(1) Particles which are demonstrable with the microscope, microscopic particles or microns (= 200 $\mu\mu$).

(2) Particles which are not demonstrable, but only optically provable, ultramicroscopic particles or ultramicrons from 200 $\mu\mu$ up to molecular size.

- (*a*) Those which may be proved as individual particles; submicroscopic particles or submicrons (to 4 $\mu\mu$).
- (*b*) Those which are not provable as individual particles, amicroscopic particles or amicrons.

The latter can excite light impressions in their movements on one another through their refracting power. With the observations of the smallest submicrons, we already reach the limits of the larger molecular units. Since the average size of an individual molecule is given as 0·6 $\mu\mu$, groups of six molecules, situated on one another, brought into the ultramicroscope arouse optical impressions. We can, therefore, by means of the wonderful instrument constructed by Zsigmondy and Siedentopf, actually peer right into the world of molecules.

The refracted forms visible in the ultramicroscope of submicrons and amicron groups appear in different colours and different degrees of clarity and show dancing, bouncing Brownian molecular movements. Whilst the ultramicroscopic investigation of larger (suspensions) colloids (colloidal metal solutions) has been much pursued and has given important results, unfortunately the investigation of protoplasm and tissue by the ultramicroscope is only at its beginning (E. Raehlman, Michaelis) and has not been carried far since a technique for the preparation of specimens which suffices for the ultramicroscope is not yet accomplished, and the few which can be studied in erythrocytes, leucocytes, and granules, do not confirm the conclusions gained from the usual microscopic study. Most recently a satisfactory method has been worked out, and through investigation in the dark-ground field a glimpse into leptonomorphology has been obtained (plasmodial form of connective tissue, Heringa, structure of fibrillæ, Schmidt).

Para. 118. That the living substance possesses the form of a reversible colloid is of the greatest importance for understanding the physiological processes of the cells (Lundegardh). We can even say " that the phenomena of the living cell are not understandable without reference to the properties of colloid " (Lundegardh). We follow Lundegardh in these presentations of the finer form, for we find that he has described these relations most clearly and impressively.

The most essential is the enormous increase of surface that occurs between the phases through the dispersion. This fine subdivision is the precursor of chemical activity. The physically heterogeneous and chemically different materials are separated from one another by the surfaces. Since in the same interval of time the masses of two different substances converted are proportional to their surfaces, there arises from the colloid condition the possibility of increase or diminution of surface, that is the possibility, through degree of subdivision, of controlling and regulating the proportions of the substances in the finest degree (self regulation, pp. 35, 301). The surface increases along with the speed of the processes of change. Herein arises a further effect of surface force which expresses itself in adsorption (accumulation of material on the surface). A colloid can exert an influence on a chemical action merely by its presence. The colloids are extremely sensitive to the effects of salts. The imbibition and the abstraction of water (sol and gel formation) are promoted by certain salts, and hindered by others. For the maintenance of the colloidal state salts are absolutely necessary. Since they are normal constituents of the plasma and the tissue fluids they regulate the change of matter. Further, the intracellular passage of material, the streaming of the plasma (convolution of the surface, adsorption diffusion processes) are to be referred to colloidal phenomena.

These processes attributed to metabolism in a general sense (p. 38) are now explained by the colloidal state in a quite different fashion than was the earlier custom. The old conceptions relating to metabolism of a protein molecule being broken down and renewed are replaced by the idea of molecular forces in general more complicated but yet localized and regulated to the finest possible point. The degree of subdivision, the presence of salts and cell ferments are the factors of this regulation. The fact that it is an "auto" regulation (the cells bring out these regulation factors autonomously, and dismiss them at their need) is the vitalism of the processes which is not explained by the colloidal form (p. 35).

The fact is most important that all these processes are somehow localized. There rests on this the fact that within a colloidal plasma, in separate areas at the same time, numerous metabolic processes can go on, without interfering with each other. This makes it possible that special formative and form maintaining factors are localized, and, speaking quite generally, are to be regarded as spatially determined. We now know that many formative processes depend on the colloidal form. Cell differentiation, like fibrillæ and granules, can be grouped as a change of state of the dissolved phase (gel formation) which, as singly repeated or periodic effects, arises as the result of subdivision and coagulation. It ought to be stated here that in the formative history of granules which arise as amicrons and grow to submicrons, we should distinguish whether this enlargement arises through clumping together (agglutination) or piling up with maintenance of the individual particles. That such formed cell-organs as fibrils, granules, centrioles, remain constant and do not again undergo dispersion, is explained hypothetically by a cuticular colloidal investment which was adsorbed by the larger particles. This removes the suspension from the influence of the dispersant. According to Zsigmondy surface tension also acts as a force by which the solution substance (fluid molecules) is fastened to the surface. The electric charge of individual particles which certainly is of importance for cellular processes involving movement (nuclear division, spindle formation, sphere radiation) and the increase of energy, which is found in the increase of surface (cell nucleus at rest), and reduction of energy found in their diminution (transference to and from nuclear areas to chromosomes), may be called to mind. It is especially in the colloidal state that the final basis of the cause of the spontaneous ageing of the cells lies. Moreover, a colloidal system is not like a solution, of similar concentration everywhere but (which can be proven in all artificial colloids) an individual type which has a history which depends on the way in which the colloid was prepared, on the types of the substance dissolved in one another, and on invisible complicated conditions under which the system exists. Here arises an important analogy between the technical and the vital colloid. In all these there arises in the course of time a flocculation of the colloid dispersum which finally produces after-effects seen in the inner or outer working (hysteresis). In the active cell a self renewal is found which puts off the hysteresis without being able to hinder it entirely. The spontaneous age and death of the cells can be regarded in the last resort as the running down (it can exhibit life only when labile) of a system striving towards a complete equilibrium.

(2) The Hofmeister Cell Model.

Para. 119. After this discussion we return to what has already been said on the form of the cell and see how much clearer our theories of structure have become. In particular the alveolar and granular theories are in best accord with colloidal nature of protoplasm. The dispersion of one substance in another must appear as an alveolar formation morphologically.

Either the water-poor phase (granules) is dispersed in a watery dispersant which then forms the wall of the alveolus, or the water-poor phase forms the alveolar wall in the coagulated condition which encloses the dispersant as droplets.

Also the granules lying in the alveolar wall and the alveolar spaces enter without compulsion into the whole scheme. The nuclear membrane can be adjudged as the limiting membrane between two different colloidal systems. The solution and the precipitation of the chromosomes can be regarded as the intermingling and the separation of two phases as above explained, and the diminution of the chromosomes as examples of marked coagulation. All this is placed within the range of microscopic visibility. There must, however, be a submicroscopic alveolar and granular structure. Therefore it follows (Hofmeister) that the real vital processes occur below the range of microscopic visibility. What we see are only quite large indicators showing that far beyond the range of visibility processes are carried out which are decisive for active and material exchanges in general, so also for the maintenance of form, form formation and form upbuilding.

The question comes into the mind if in the infinitely tiny cavities of a colloidal system there may be sufficient actual space for the innumerable energy and form-forming centres side by side. Our mind can more easily comprehend infinite size as "infinite" or think of a whole milky way in a star mist, than it can comprehend the same infinity in smallness or think of a granule as a cosmos. One can now, according to the plan of Hofmeister, seek to build an approximation to this infinity in miniature by enlarging the cell dimensions to a huge extent. One attains, then, a cell model in whose interior one can then place one's self.

Hofmeister reckoned a liver cell of man as of 20 μ width and a cubic content of 8,000 cb. μ. He showed further that in this cell there could be about 200,000 milliards of molecules of water, 2,000 milliards of molecules of crystalloids and salts, 200 milliards of protein molecules and lipoids in colloidal form.

He now asks, How large must a cell be if one assumes that the size of a molecule is equal that of an ordinary brick? He gives then a figure of about 7,000 square kilometres at the base and 50 m. in height. This giant structure would afford accommodation for the 200 milliards of protein, fat, crystalloid, and salt molecules as walls, floor, roof, walls and objects in the interior (that is as watery-poor phase) and between the water molecules there would be living rooms, working rooms, passages, steps, stairs, etc. "The protoplasm of a cell of average size furnishes the necessary structure whose complication far exceeds that which must be expected only on anatomical grounds." At the same time Hofmeister reckoned the size of a submicron of 0·1 μ according to the same proportions as equal to a factory of 100 m. long, 20 m. wide, and 20 m. high. A granule which lies at the limits of microscopic recognition (0·24 μ) we can reckon in this cell model as a hill of 150 m. transverse diameter and there would be room for about 4 million of these granules in the model.

According to Hofmeister's example, we can also reckon that a human ovum would include an area which would extend over the whole Pfalz and Saar territory with the height of the Eiffel tower. The smallest visible granules would be hills of 150 m. width, the centrioles and the chromioles would be 200 to 250 m. in transverse measurement.

Such a model provides a conception of the cell if it is thought to be constructed as complex colloid system. Strong walls traverse the enormous space formed as alveoli of the size of small mountains. Within this, in submicroscopic areas, there lie first dispersed in water the special elementary bearers of life. The principle, according to which these chambers are arranged, is yet unknown. It is certain that the innumerable different assimilatory and formative processes are undisturbed by one another. The central body of the size given above can be a giant magnet giving order to the whole. The rays of the sphere, which the chromosomes displace in their division, would be streams against which the great floods of the earth would be insignificant. Within this system the nucleus swims. The phantasy might paint the interior in lively fashion. It could be in each case arranged that the active part of the chromosomes, the gene, might be represented as a relatively large element of definite form and quality or quite generally as definite localized energy-spenders.

It is customary, as Hofmeister says, to take an organism of this type as the simplest member at the beginning of the development series. The idea of the cell model developed here brings us necessarily to the conclusion that the cell must start from simpler elementary life-bearers with a capacity for individualized existence and propagation. However, we do not know these stages which Nature has not preserved for us so far as we can see. On the other hand, doubts based on the existence of ultramicroscopic organisms have recently been expressed, because each living system must have a definite minimal size, so that the molecules to perform the vital processes necessary may have space in sufficient amount. One has experimentally (Miehe) estimated this size at 0·2 μ, that is at the limits of visibility. Whether, within the cell, life is present in ultramicroscopic particles is doubtful, just as the existence and the possibility of existence of ultramicroscopic organisms is doubtful.

(3) Conclusion. Microscopic Structure and Morphology.

Para. 120. It is the privilege of the imagination to form a picture like this, since actual knowledge of the microscopic structure of the cell is not yet possible for us. However, one purpose of investigation at least is to describe the problems whose answer is the purpose of the future. According to what principles do the molecules of a cell assemble in order to form the organism? The answer so far as we can see at the moment lies in only two possibilities, both of which are now presented hypothetically. The theories which are alone valid can be distinguished as meroplastic and holoplastic.

The meroplastic puts the cells as an aggregate of entities; the holoplastic, on the contrary, regards the cell as the entity. According to this the distinction is the presence of a meristically divided germ plasm, which is seen in the chromosomes and their hypothetical constituents, the chromioles. The chromosomes are indestructible individually. They have in the cell a parasitic existence. Somewhere and somehow the genes are localized in them. In the holoplastic idea the whole cell is a very large chemical body which can be referred to a giant structural formula. It needs to possess a central nucleus with complex accumulated side chains. According to the accumulation of these side chains, and according to the position of the atom in the molecule of the side chain (Fick) there are gradations of structural form. The individual would even be the individual structural formula (individual plasm, Fick). In a collection of molecules, for example, of twenty building stones the number of isomer connections which can be derived through the series of building stones would be two and a half trillions. Therefore the isomers arise within the building stones themselves (Abderhalden, in Grosser). For this theory the chromosomes are only visible indices of the structural form from which something follows, just as the leptonological characters of the crystal follow from the characteristics of the mother form. All that we call "primordia" would rest on the structural peculiarities of the individual plasma. The final individual graded characters (ridges on the fingers, skin nævi) would be only the finest and the last reaction of a specific structure of the whole primordial substance.

Each of the two theories would be reconcilable with what we know. The meroplastic theory offers us the handier symbols. The holoplastic would make many questions now difficult much easier, such as phylogenetic growth, phylogenetic unfolding, and before all the relationship between phylogeny and ontogeny. Moreover it can be demonstrated that the more firmly anchored nuclear portion of the structure changes less, or certainly not more, so that the new formations are split off from the peripheral chains and in the course of the phylogenetic history would be situated more and more centrally. Therein lies the possibility that a change can penetrate the formal structure of the whole and its specificity. Such ideas conform particularly to Plate's theory of inheritance stems. How the difference between these two theories will affect morphology we cannot say at this moment. We can say this much only, that recent knowledge of the colloidal form of protoplasm is reconcilable with the idea of definite structures, the finest structures classifiable as morphological. One recognizes differences of structure in protoplasm through the different distributions of the watery phase causing dissimilarities first only in a gross form (Spiro). However the old micellæ theory of protoplasm of Nägeli, which was a true structural theory whose value has for a long time been limited (v. Ebner), has become again of importance through these colloidal ideas (Zsigmondy). According to Nägeli protoplasm is made of larger elements, which he calls micellæ (from mica, a crumb), according to the form of a crystalline solution. The micellæ arise from the growth of smaller molecular units and are separated from one another by layers of fluid.

Recent colloid chemistry has largely confirmed the theory of Nägeli. Indeed protoplasm behaves like a solution of colloidal gold in which the particles remain separate from one another by being covered by a layer of colloid.

Both, the protoplasm and the gold solution, consist of these particles, not permeated by solution, and separate into them when destroyed. This "primary particle" (Zsigmondy) need not be the "final" particle since it can be formed from molecules (like the micellæ). It is known that the secondary particles arise from the primary particles by growth and fusion along with diminution of the degree of dispersion. So they arrive in the field of visibility. Also for the products of the plasma, e.g., the doubly refracting fibrillæ of the connective tissue, formation has been proven through apposition of the primary particles (Schmidt).

In regard to the finer form of protoplasm the following can be taken as certain. (1) Accumulation of specific molecular units. (2) Topographical division of these units. (3) Integration of the whole in the sense that (4) new formation and growth bring out the whole structure according to their distribution. So far as we can see, the solution of the structural laws lies along the lines of the holoplastic rather than the meroplastic conceptions.

The proof of the micellæ units typical for each type and the regulation of growth and subdivision will be the last and final purpose of cell investigation [para. 102]. Only then shall we be able to see in what relation these structures stand with the known cell structures (chromosomes, cell nucleus, cell body). Also then it will be possible to follow the transformation of structural forms into the formation of tissues, the fibrillæ, the ground substance, etc. There would then be a conception of histogenesis, which as a consequence of a principle, as a deduction of form, would erect histology into a true science.

Also the form of the whole [paras. 25, 90] which, as we have seen, can now be formed in intimate promorphological relation to the elements, will then be recognizable as a function of the structural formula. It will be possible to treat the forms themselves and the changes of form in a higher degree, than is now believed, from the knowledge of the fundamental formula here deduced. Perhaps it will be possible to demonstrate the individual plasma stereochemically; we could imagine it placed before us as clearly as the skeleton in a museum of the future. Then for the first time would exact morphology be possible. We would have then, so to speak, the organic in the crystal. The deepest significance of the organic reveals itself to us here for the first time. It signifies the maintainance of the structures in the fluid of the changes of form. This is doubtless the real vital fact wherein Goethe has seen the secret of all life [cf. also para. 92]. We have accustomed ourselves to see the living phenomena in the individual being in the course of its development. For us they coincide with the physiological; the life follows death. However, as an individual being we can ascribe only to man a unique value because this unique value is his ethical nature. Beyond this, individual organisms are little or nothing; the form is everything. That which works in the maintenance of structure, brings it nearer to perfection, and thus makes possible even the loftiest actions of the greatest heroes of the human race, this too is life and the real essence of life. Life, morphologically considered, is free from the compulsion of the ætiological, free from growth and decay; it is perhaps on some glimmering of this that man's conviction of the indestructibility of his being is based.

The anatomy of man places its objects of investigation in relation to all other forms. If the relation as such is known in general only scientific anatomy can investigate it in detail and demonstrate its growing boundaries. It remains, therefore, a science within the limits that are set to every science by the limits of experience. How the great connected scheme of organisms, outside empiricism, is to be represented and how we are, from this point, to assess the preservation of form, is no unimportant question, but it is one that lies beyond the limits of the task which science ought to set itself, however far morphology may prepare our minds for such further problems.

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